An Unexpected Journey: the Biogeography and Conservation Ecology of the Trapdoor Spider Genus *Cantuaria* Hogg, 1902

A thesis
submitted in partial fulfilment
of the requirements for the Degree of
Doctor of Philosophy

at
Lincoln University
by
Victoria Rose Smith

Lincoln University
2016

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The genus *Cantuaria* consists of 42 currently recognised species, all of which are endemic to New Zealand (NZ). *Cantuaria* spiderlings build their burrows near to their mothers, and usually remain there for life.

Cantuaria's sedentary life history is at odds with its distribution, which reaches from Stewart Island up to Whanganui. *Cantuaria*'s sister genus *Misgolas* Karsch, 1878 is found in Australia. In this thesis, I used a dated multilocus Bayesian phylogeny to reconstruct [1] when the most recent common ancestor (MRCA) of *Cantuaria* diverged from *Misgolas*, and [2] the distribution history of *Cantuaria* within NZ. My results showed that *Cantuaria* and *Misgolas* shared a MRCA as recently as 18 million years ago, indicating long distance dispersal in *Cantuaria*'s biogeographic history. However, there was also evidence to suggest that vicariant geographic barriers interrupt dispersal, as species to the east and west of the Southern Alps share a most recent common ancestor approximately 5–8 million years ago. The genus appears to have originated in the southern part of the South Island, before moving gradually northwards.

Cantuaria phylogenies were used to delimit species using the Poisson tree process, and 12 new species are described. Morphology and phylogeny do not concur, and geographic location combined with DNA are the most reliable methods for identifying *Cantuaria* species.

Due to *Cantuaria* species' small populations (defined as a semi-isolated individual or group of individuals) and lack of dispersal ability, I hypothesised that they would be susceptible to habitat loss and disturbance. My research investigated how different types of habitat and disturbance affect *Cantuaria* population presence/absence. I also assessed the threats that may be facing individual populations. A taxon that is easily susceptible to changing environmental parameters may be less likely to survive and colonise new territory after a long-distance ocean crossing. My results show that *Cantuaria*, surprisingly, are able to breed and reproduce in a variety of habitat types, but they are found less often in areas with very high rainfall, and in high elevation areas. Some populations appear to contain very few individuals, and may be

threatened by habitat destruction. The threats to *Cantuaria* populations include climate change (which may increase rainfall in some areas) and urbanisation.

A meta-analysis of biogeographical research from the last decade for all taxa investigated the factors that may affect a species' biogeographic history in NZ and found no evidence to suggest that characteristics, such as dispersal ability, affect a species' biogeographical history over evolutionary time.

Keywords: Biogeography, Idiopidae, idiopids, Mygalomorphae, mygalomorphs, ancient, dispersal, vicariance, random forest, niche modelling, beetling, Oligocene drowning, Oligocene

Acknowledgements

The last three years were never unenjoyable. I can attribute the good humour that I felt throughout my PhD entirely to the excellent support that I had from supervisors, funders, and my friends.

First I thank my supervisory team, Adrian Paterson, Rob Cruickshank, Emily Fountain and Cor Vink, for giving me free rein over this project. They were there if I had questions or needed help, but I had a great deal of freedom to explore and research in my own way. Myles Mackintosh was a fantastic support to the project, going above and beyond his job with seemingly effortless efficiency.

This work was funded by a generous fellowship from the Miss E L Hellaby Indigenous Grasslands Research Trust. The Mohamad Bin Zayed Species Conservation Trust, Lincoln University, Gordon Williams, Otago Museum, and the Brian Mason Trust all provided grants towards the completion of this research, for which I am most grateful.

My family was supportive throughout my PhD; thank you. My friends, including Dave and Shirley Lawry, became a different sort of family. Thanks to Rob Lawry for his friendship, help, and excellent ability to handle falcons and many different species of roadkill. My good friend Nathan Curtis provided me with a sense of perspective, and some stability in the form of a place to live. Thanks also to the games group Tim, Laura, and Sam for making Fridays awesome. Johannes Welsch was a frequent reminder that one can undertake a PhD journey in style, and that there is always time for a nice cup of coffee and a sit down.

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Chapter 1
Thesis context

"We don't want any adventures here! You might try over the Hill or Across the Water."
-J. R. R. Tolkien, The Hobbit

Understanding historical distributions of species and land masses can increase our knowledge of the ways in which species react to change on different scales (Jones & Rebelo 2013). Biogeography incorporates ecology, genetics and geology to understand the history of a geographical area and its inhabitants. For example, combining genealogies into a phylogeny to trace both deep and recent divergence enables the pattern of evolution to be discerned; applying a molecular clock to the phylogeny adds context so that geological processes can be incorporated into analysis (e.g. Beck 2008; de Boer, Steffen & Cooper 2015; Liu et al. 2016; Schaefer, Heibl & Renner 2009).

Ecological data can provide phylogeographic evidence to supplement a phylogeny. For example, if a focal species and its related taxa currently have very specific habitat requirements, the focal species is less likely to have previously been distributed in habitat that does not meet its current requirements (Crisp, Trewick & Cook 2011; Toon et al. 2010).

Biogeography may help us to predict species' responses to present and future developments, such as climate change, by discovering how species reacted to previous changes in their environment. Collecting data on species distributions and habitat requirements also facilitates evaluation of a species' conservation status, and areas that should be preserved if the species is endangered (Belbin 1993; Burns, Innes & Day 2012; Buse, Schröder & Assmann 2007; IUCN 2016; Ward et al. 1999; Watt 1979).

The trapdoor spider genus *Cantuaria* Hogg, 1902 (Mygalomorphae: Idiopidae) is endemic to New Zealand, and distributed from Stewart Island up to Wanganui in North Island (Forster & Wilton 1968). Their populations are separated by mountain ranges, large water bodies, and heterogeneous habitat. Like most mygalomorphs, *Cantuaria* show limited vagility: upon leaving its mother's burrow, a spiderling disperses only a short distance, by walking, before building its own burrow where it will remain for life. Males, upon reaching adulthood, leave their burrows to search for females (Marples & Marples 1972; Todd 1945). The fossorial natural history of *Cantuaria* spp. raises questions as to how it arrived in New Zealand (most evidence supports dispersal from Australia as the general origin of New Zealand species; Goldberg, Trewick & Paterson 2008; Trewick, Paterson & Campbell 2007), and how it reached its current distribution. Little research has been conducted into the biogeography and ecology of

Cantuaria spp., though they are assumed to have been part of New Zealand's Gondwanan ancestry (Irish 2001).

1.1 Research aims

This thesis focuses on the biogeography of *Cantuaria*. My overarching aim is to uncover when and how *Cantuaria* arrived in New Zealand and spread to its current distribution, by combining geology, genetics, and ecology. The current taxonomy of the New Zealand Idiopidae will also be investigated using molecular evidence, focusing primarily on describing new species found throughout the course of this study. Conservation issues will be raised through the process of my biogeographic study, enabling investigation into the past, present, and future of New Zealand's enigmatic trapdoor spiders.

Chapter 2
General introduction

2.1 New Zealand biogeography

New Zealand is an emergent fragment of a much larger, mostly submerged, continent called Zealandia. Zealandia was attached to Australia as part of Gondwanaland until approximately 80 mya, when the two continents split (Mildenhall, Mortimer, Bassett, & Kennedy, 2014; Trewick, Paterson, & Campbell, 2007; Wallis & Trewick, 2009). Over time, Zealandia gradually stretched, thinned and sank, becoming mostly submerged approximately 25 mya (Mildenhall at al. 2014; Wallis & Trewick 2009). After this period (known as the Oligocene drowning), tectonic activity caused New Zealand to rise out of the sea (Mildenhall et al., 2014), and it was colonised by flora and fauna.

The Oligocene drowning had a massive influence on New Zealand's modern fauna. Previously, biologists assumed that New Zealand's flora and fauna were mostly derived from "Gondwanan" lineages that were present when Zealandia and Australia were part of Gondwanaland (Bellamy et al. 1990). However, molecular and geological evidence suggests that many of New Zealand's lineages arrived there more recently, by dispersal from Australia or other neighbouring continents (Biffin, Hill & Lowe 2010; Cooper et al. 2001; Giribet & Boyer 2010; Trewick et al. 2007). Even fauna previously considered to have little dispersal ability, such as kiwi (*Apteryx* spp.), are likely to have arrived in New Zealand within the last 20 million years (Cooper et al. 2001; Mitchell et al. 2014). Proving that New Zealand's species have all arrived by dispersal after the end of the Oligocene drowning is impossible, but the evidence gathered so far appears to support dispersal as being more frequent than vicariance in the history of New Zealand's modern fauna.

Some biogeographic evidence suggests that New Zealand's freshwater crayfish (Toon et al. 2010) and mite harvestmen (Boyer & Giribet 2009) did not disperse to New Zealand, and may therefore be genuine "ghosts of Gondwana" (Gibbs 2006). Freshwater crayfish and mite harvestmen have low vagility, highly restrictive habitat requirements, and show a high degree of short-range endemism. These characteristics may reduce their likelihood of having dispersed across the Tasman Sea; low dispersal ability makes ocean crossings less feasible. Researching the genetics and distributions of other locally endemic taxa improves our understanding of the ghosts of Gondwana, and what they can tell us about the history of New Zealand.

2.2 Mygalomorphs as model organisms for studying biogeography

Mygalomorphae is an ancient (300 myo; Ayoub et al. 2007) infraorder of spiders that possess ancestral traits, such as paraxial chelicerae and two pairs of book lungs. The sister taxon to

Mygalomorphae is the most diverse spider suborder, the Araneomorphae. While araneomorphs generally have high vagility (for example, ballooning; Bell et al. 2005), mygalomorphs usually have little dispersal ability, even if they can balloon for short distances (Bell et al. 2005; Coyle et al. 1985). For example, two populations of *Antrodiaetus riversi* Cambridge 1883, a Californian trapdoor spider species, were shown to have been separated by the Central Valley 2–3 mya. Despite *A. riversi*'s lack of dispersal ability, the populations appear to have become temporarily linked once more, approximately 1.2 mya (Hedin, Starrett & Hayashi 2013). The low vagility of *A. riversi* has facilitated the preservation of historical biogeographic signal, enabling research into the link between a species' evolutionary history, and the geological processes in its environment (Hedin et al. 2013). Many other studies have focused on the biogeography of mygalomorphs, usually finding them to be excellent models for biogeographical study (e.g. Bond et al. 2001; Bond & Stockman 2008; West, Nunn & Hogg 2012). Low vagility, combined with high habitat specificity (Ferretti et al. 2012; Hedin et al. 2013), makes Mygalomorphae excellent candidates for biogeographical research. However, some Mygalomorphae are able to disperse longer distances by ballooning, such as *Atypus affinis* Eichwald 1850; their higher vagility facilitates gene flow between populations, so that geological processes have less influence on the distribution of ballooning mygalomorphs. However, ballooning ability does not preclude highly selective habitat requirements or complex biogeographical history (Pétillon et al. 2012). *Cantuaria* spp. are short-range endemics, and are not known to disperse by ballooning (Irish 2001; Marples & Marples 1972). Their lack of vagility, combined with their wide distribution, makes *Cantuaria* an interesting genus for biogeographical research.

2.3 The genus *Cantuaria*

Cantuaria is an endemic New Zealand trapdoor spider genus, containing New Zealand's only representatives of the family Idiopidae. *Cantuaria* are fossorial, with populations forming clusters of burrows, each one of which is assumed to contain one adult spider (although *C. huttoni* burrows can be branched and have more than one entrance (M. Wakelin, pers. comm.), and other species may be the same). Species within the *huttoni* group have almost perfectly circular holes, with edges either flush with the surrounding substrate surface or slightly raised. Silk may be faintly visible inside the mouth of the hole, and there may be a garden of arranged substrate particles around the entrance of the hole, secured with silk. In some areas (e.g. Stewart Island), half of the burrow perimeter is extended into a flap-like wall, which may be physically pulled down by the spider when disturbed. Species outside the *huttoni* group have, on average, larger (≥ 10 mm) burrow entrances, concealed by a cryptic lid. The lid is at least vaguely circular, constructed from substrate and silk, and secured by a hinge of silk. Sometimes a pile of soil, excavated by the spider, will be in front of the lid. *Cantuaria* burrows are particularly cryptic, and in some substrates may only be found by touch. Lifting a suspected lid will confirm the presence of a burrow, as beneath will be a tunnel with an almost perfectly

circular cross-section, smooth on the inside with the appearance of having been chiselled or milled (as opposed to the rougher-looking tunnels constructed by *Stanwellia* spp.). The topmost few cm of the tunnel are usually lined with silk (Forster & Wilton 1968; Irish 2001; Marples & Marples 1972; Todd 1945).

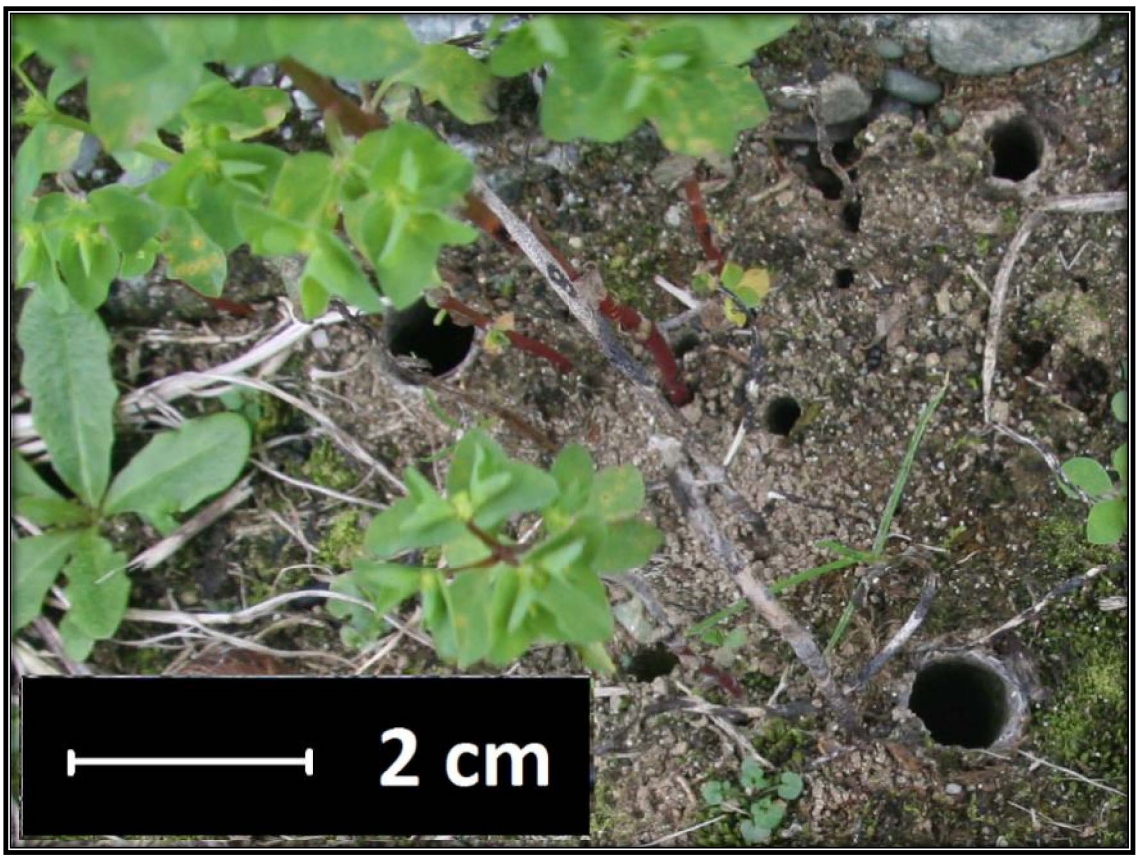

Figure 2.1: A population of *huttoni*-type *Cantuaria* in Tuatapere, showing adult and juvenile burrows close together.

Cantuaria offspring are raised in their mothers' burrows. A mother *Cantuaria* cares for her offspring by providing them with food and protection for six to 18 months (Irish 2001), until they are large enough to catch their own prey (normally consisting of terrestrial insects; Irish 2001). Spiderlings leave their mothers' burrows en masse (pers. obs.). A *Cantuaria* spiderling does not walk far before building its own burrow in the immediate vicinity. As the spider grows, it widens its burrow, but does not leave. Upon reaching adulthood, a male *Cantuaria* will leave its burrow to search for females, but a female remains in the same burrow that it built as a spiderling, growing, feeding, mating and raising spiderlings in the same burrow not far from its mother.

The distance covered by male *Cantuaria* on their search for females is unknown, but most likely they disperse by walking, so are unlikely to cross large distances or barriers (Irish 2001; Marples & Marples 1972). The lack of dispersal ability in *Cantuaria* spp. has led to dense clusters

of individuals in a population, sometimes with burrows only a couple of centimetres away from each other (see Fig. 2.1). Forty-two *Cantuaria* spp. have been described (World Spider Catalog 2016), and approximately 20 undescribed species are thought to exist (R. Raven, pers. comm). The taxonomic status of the genus is uncertain, however; Forster (1968) and Paquin et al. (2010) speculate that *Cantuaria* spp. may not be congeneric. There are two ecotypes, which may be separate genera, but are currently referred to as the *huttoni* and non-*huttoni* groups (Forster & Wilton 1968). Non-*huttoni* species make up the majority of species in the genus, and are characterised by their female genitalia, which consists of two elongate lobes. Burrows built by non-*huttoni* species generally have trapdoor lids. Non-*huttoni* species are distributed as far north as Whanganui, and as far south as Balclutha, occupying a range of habitats from semi-arid scrub to rainforest. Unlidded burrows are built by all *huttoni* species (although some build small, wall-like partial lids; Fig. 2.2), which tend to inhabit moist to very wet areas, and have dome-shaped female genitalia (see Fig. 2.2). They are distributed from Stewart Island to Banks Peninsula (Forster & Wilton 1968). Most literature simplifies the ecotypes, stating that *huttoni* species inhabit forests and non-*huttoni* species inhabit grasslands (Forster & Wilton 1968; Marples & Marples 1972). At individual level, *Cantuaria* spp. do not appear to move around much, remaining in their burrows for the majority of their lives; at the population level, they form small, dense patches of individuals. However, populations within a species can be widespread: for example, *C. johnsi* populations are spread over 110 km apart (see Fig. 2.3).

The distribution of species within the genus is surprisingly wide for organisms with such low vagility. The different species are separated by mountain ranges, braided rivers, and huge tracts of land and water (see Fig. 2.4; Appendix F). New Zealand is geologically dynamic; in the last three million years, Stewart Island has become separated from the South Island, where it was previously joined by a land bridge; Banks Peninsula, previously an island, has become connected to the mainland; and the North Island has grown to include the Taranaki, Wanganui and Wellington regions (S.A Trewick & Bland 2011). Stewart Island, Banks Peninsula, Wellington and Wanganui all have locally endemic species of *Cantuaria*, as identified by Forster and Wilton (1968). Investigating the origins of these endemic lineages may shed some light on *Cantuaria* dispersal ability, in particular whether they may have crossed the Tasman from Australia.

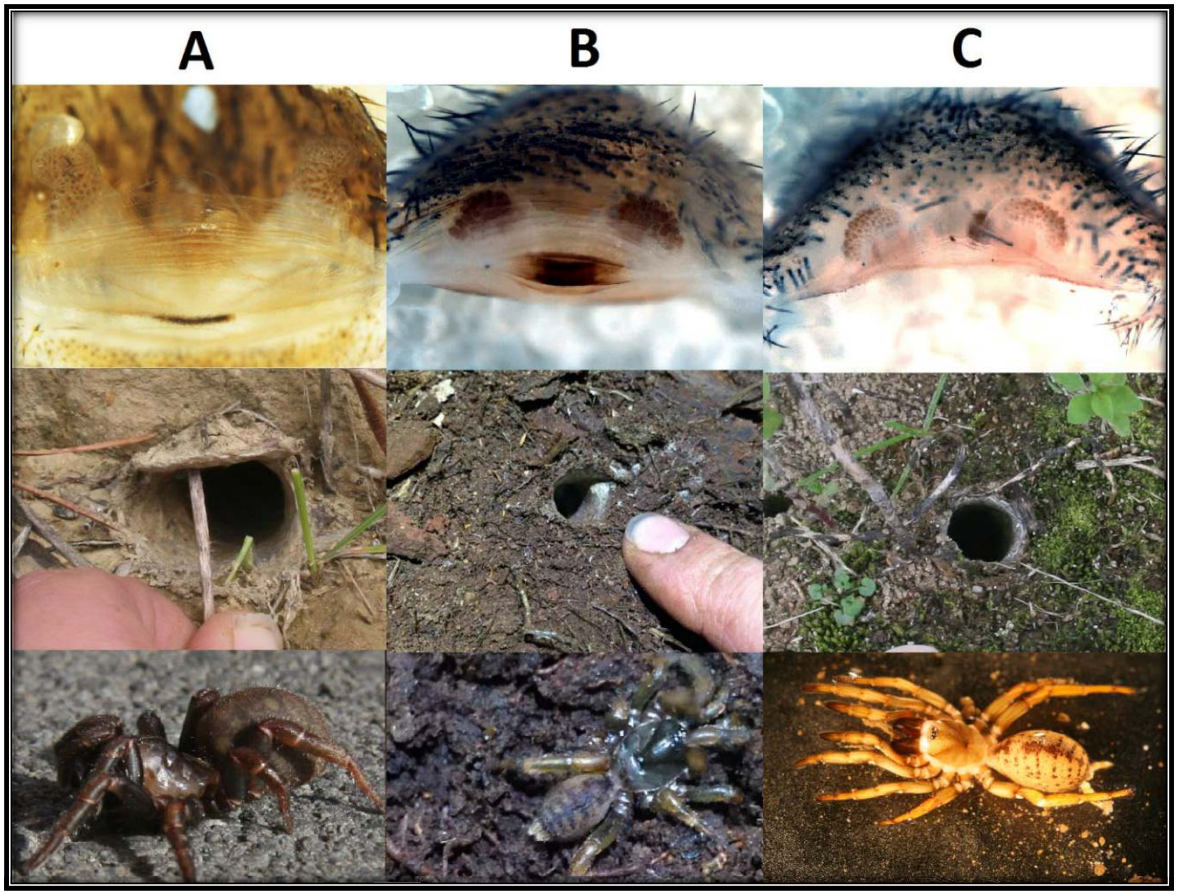

Figure 2.2: Two ecotypes within the genus *Cantuaria*: non-*huttoni* (A) and *huttoni* (B, C). While most *huttoni* spp. do not build lidded burrows, some build partial lids (B). The top row of images shows typical female genitalia for each type, the middle row shows typical burrows built, and the bottom row shows the whole animal.

Figure 2.3: Map showing the distribution of *C. johnsi* At Golden Bay and the northwest coast of New Zealand (black and white circles) The populations are separated by mountains, rivers, and large tracts of land.

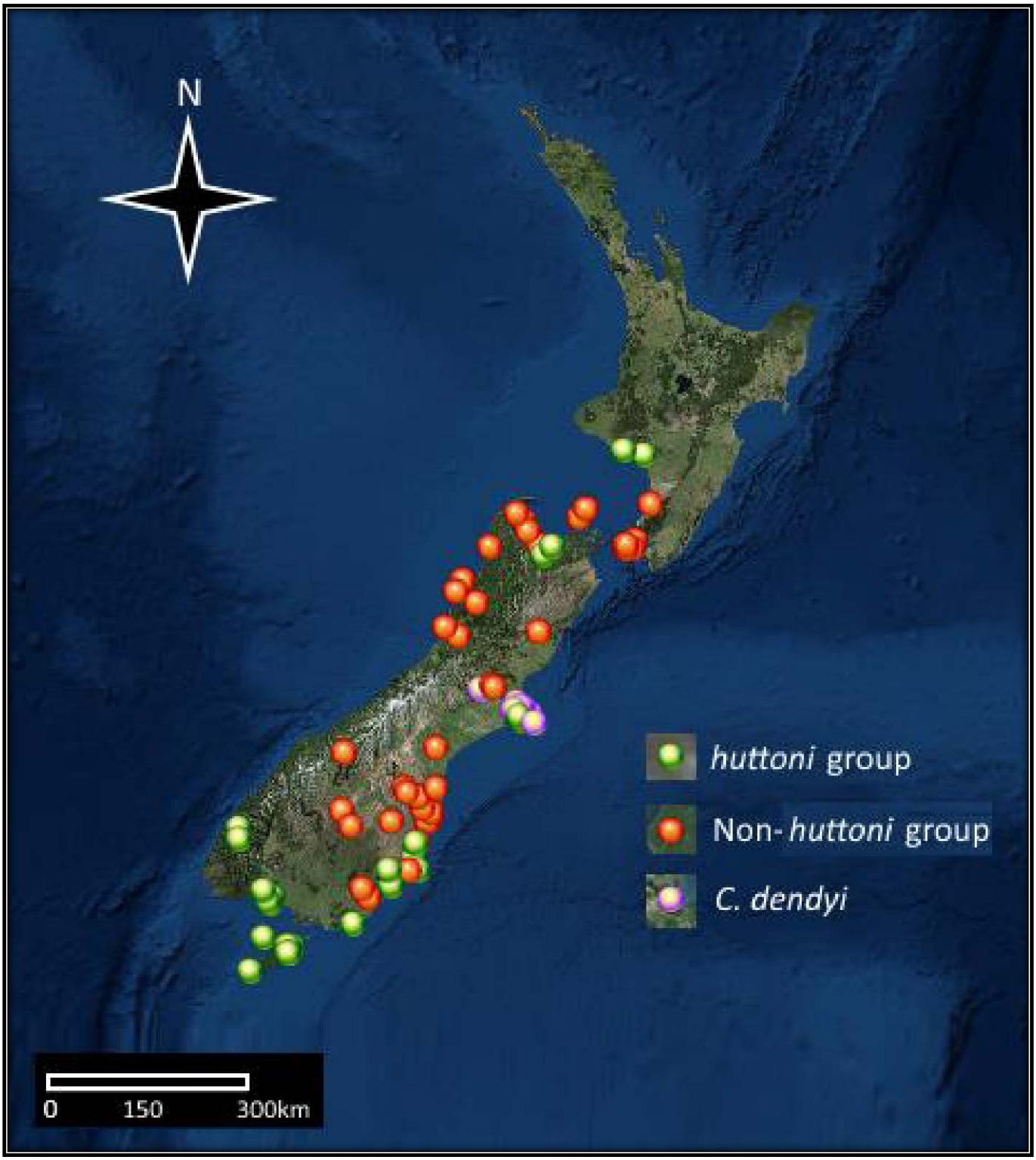

Figure 2.4: The known distribution of the genus *Cantuaria* in New Zealand. For range comparison, the two major ecotypes (*huttoni* group: green and non-*huttoni* group: red) and the type species (*C. dendyi*: purple) have been colour coded separately. A full list of specimens and their collecting locations is given in Appendix F.

Cantuaria is an ecologically important genus,as an arthropod predator, a food source for birds, and a host for parasitic worms and wasps (Irish 2001; Marples & Marples 1972). Trapdoor spiders also form part of New Zealand's rich and unique biodiversity. However, the small size of *Cantuaria* populations, coupled with their apparently low ability to colonise new habitat, may spell an uncertain future for some species of *Cantuaria*. My research aims to increase our understanding of the ecology and biogeographical history of *Cantuaria*. In addition to providing evidence regarding New Zealand's biogeographical history, my research may inform future efforts to protect *Cantuaria* spp. and their habitat.

Chapter 3
New Zealand biogeography

3.1 Introduction

Biogeography is the study of species distributions in space and time. As a science, it has grown from religious justifications by Linnaeus (C. B. Cox & Moore 2010a), through observations by Humboldt (1805), Darwin (1859) and Wallace (1876), into the collaboration between ecologists, geologists, and evolutionary biologists that it is today. Globally, biogeography has received renewed interest, with oceanic islands, such as Hawai'i, serving as models (e.g. Nelson & Platnick 1981). Of particular interest to biogeographers is the study of vicariance (a new geographical barrier fragmenting a previously widespread distribution) and dispersal (individuals from the population crossing a preexisting geographical barrier; Sanmartín 2009) (Nelson & Platnick, 1981). The definitions of biogeography and its related terms (e.g. dispersal and vicariance) have changed over time; this chapter uses recent definitions (Cox & Moore 2010) (Fig. 3.1).

Global biogeography, its history, and its findings have been reviewed in a book, *The Monkey's Voyage* (de Queiroz 2014), which highlights particular issues to consider when critically evaluating biogeographical literature for any particular taxon. First, conclusions are drawn in the literature from a wide variety of evidence. Inferences made purely from the biology of a single animal species can appear convincing and thus persist without question. For example, frogs were long thought incapable of crossing oceans due to their inability to withstand osmotic stress from saltwater. However, discovery of species only recently diverged from relatives overseas has suggested that basing conclusions entirely on an animal's perceived ability to cross oceans is unwise (Bell et al. 2015; de Queiroz 2014; de Queiroz 2005; Vences et al. 2003).

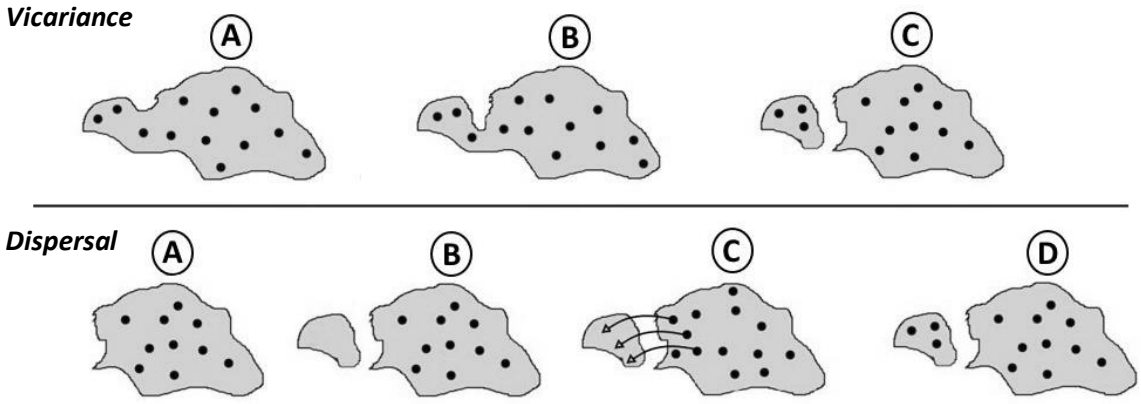

Figure 3.1: A hypothetical situation illustrating the differences between dispersal and vicariance. Black dots represent individuals of a species; the grey forms are the landmasses on which they live. Arrows indicate the physical movement of individuals. Vicariance: A) This vicariance event begins with a single landmass upon which lives a species. B) A strong ocean current begins to erode away part of the landmass. Individuals remain distributed either side of the inlet that has formed. C) The current has eroded a channel through part of the landmass; there are now two islands. Individuals are on both islands, but they have not moved relative to the landmasses on which they stand. There is no gene flow between the two islands, and the two recently separated populations may diverge and speciate. Dispersal: A) This dispersal situation also begins with a landmass upon which lives a species. B) A new island forms, for example, due to a volcanic eruption. C) At some point there is a rare event in which the species begins to colonise the newly separated smaller island, dispersing there by flying, swimming, or drifting on flotsam. D) There are now two islands, and the population has spread onto the smaller island. There may be some gene flow between the two subpopulations, but there is sufficient genetic separation for each subpopulation to adapt to its local surroundings. In time, they may diverge and speciate.

There are many methods of trans-oceanic dispersal, from swimming (e.g. black rat *Rattus norvegicus;* Harris et al. 2012; Russell et al. 2008) to using temporary sea ice as a bridge (e.g. polar bear *Ursus maritimus;* Gaston, Gavrilo & Eberl 2012). Aerial animals may fly between landmasses (e.g. black-winged kite *Elanus caeruleus;* Balbontín et al. 2008), or be blown by the wind (e.g. lycosids; Vink & Paterson 2003). Other species that are not normally aerial may be carried by flying individuals. Even relatively slow-moving, terrestrial animals, such as snails, may cross great distances over oceans if carried by birds (Vagvolgyi 1975). While the chance is remote of any one individual crossing a great distance over ocean, and surviving to reproduce (which may involve locating a mate who has likewise survived the trip) in a new habitat, the odds reduce when the timescale of millions of years is taken into account. Rafting across oceans on flotsam can be a particularly successful method of dispersal, although the direction of movement depends heavily on ocean currents. Much of Madagascar's vertebrate fauna, for example, arrived there by rafting from Africa, but their historical arrival times vary depending on ocean current direction (Samonds et al. 2012). Ocean currents and predominant wind direction tend to be relatively stable and predictable over evolutionary time, and have a large impact on the direction in which biota can disperse. Examining the patterns of wind and ocean currents in the general area of interest can enable some prediction as to the source of the biota

that are found there (de Queiroz 2014; Sanmartín & Ronquist 2004). Many studies have included discussion of possible factors affecting the ability of a species to disperse across oceans (see Curtis (2011) for a review; Close et al. 1978; Fox 1973; Gibson, Atkinson & Gordon 2006; Thiel & Gutow 2005).

Research into the abilities of organisms to undertake and survive dispersal across oceans has included the effects of wind and dispersal mechanisms on fungal spore dispersal, using theory and speculation (Dijksterhuis & Samson 2007). Other studies have focused on abilities of organisms to survive conceivable threats caused by long-distance dispersal, such as desiccation and starvation (Hopkin 1997; Weldon & Taylor 2010), and extreme temperatures (Hoffmann, Sørensen & Loeschcke 2003). More practical studies have tested the ability of invertebrates to survive floating on, or immersion in, seawater for extended periods of time (Coulson et al. 2002; Darwin, 1859; Hawes et al. 2008). The aerial dispersal of arthropods by birds has been documented (see Green & Figuerola 2005 for a review): chironimid larvae have been found to survive the gut passage of birds, leading to speculation that individuals may travel further as larvae inside bird guts than when they are winged adults (Green & Sánchez 2006). Another study found that live aquatic invertebrates were transported by birds in the gut, and could conceivably be transported in soil particles attached to the birds' feet and feathers (Frisch, Green & Figuerola 2007). The findings of papers assessing the ability for organisms to be transported long distances over oceans are valuable for theorising what adaptations could aid long-distance dispersal.

Possible additional traits that might improve a species' ability to travel long distances include an innate dispersal ability. Floating on debris may be a viable dispersal method for many taxa while others may be limited. For example, a species which must drink nectar several times a day to survive may not be able to withstand several days at sea. Some species may be able to withstand the journey, but be unable to establish upon arrival. For example, juvenile wandering albatrosses habitually cover over 100,000 km in their first year, covering large oceanic areas and encountering different land masses (Åkesson & Weimerskirch 2005). The albatross' ability to undergo trans-oceanic journeys is facilitated by its ability to fly, wing morphology, and soaring techniques (Suryan et al. 2008). Albatrosses survive dispersal over long distances due to their adaptations to oceanic life, such as ability to excrete salt through a specialised salt gland, and their diet of marine animals (Suryan et al. 2008). However, albatrosses are limited in their breeding range due to their restricted colonising ability. Their nests are often restricted to particular types of cliff area, and they depend upon particular bathymetry and ocean currents to feed their offspring (Wakefield et al. 2011; Warham & Bennington 1983). Conversely, brown rats may have limited unassisted dispersal ability, but can survive in many different types of habitat, particularly when associated with humans (see Traweger et al. 2006 for a review). They have colonised every continent except Antarctica, largely due to anthropogenic processes

(Harris et al. 2012). Ability to survive in different types of habitat may therefore also be a trait associated with dispersal rather than vicariance.

Methods of studying biogeography have changed. With increased understanding of the many different ways in which lineages may have reached their current distributions, biogeographers can focus their questions to ensure testability (Crisp, Trewick & Cook 2011). While previous conclusions regarding the origin of an area's biota may have been drawn based on its biology or monophyly, modern molecular tools allow the dating of nodes within a phylogeny. The date of divergence of a particular node is the date when the ancestral gene lineage diverged into two lineages (Heads 2005), which often happens as a result of some individuals of a species becoming geographically separated from other individuals of the same species (allopatric speciation; Hoskinet al. 2005). The date of divergence of the two species is therefore approximately the date that they became geographically separated, assuming that speciation was allopatric (Losos & Glor 2003). The application of molecular clocks has suggested that inferring vicariance based on tree topology alone is flawed (Crisp et al. 2011). For example, NZ diplodactylid geckos are monophyletic, but applying a molecular clock shows their divergence from Australian Diplodactylidae to post-date the opening of the Tasman sea (Nielsen et al. 2011). The literature is heavily punctuated with conclusions that are deceptively assertive. Even fossil evidence can be misinterpreted, particularly when fossils are difficult to place taxonomically (Ronquist et al. 2012). For example, Mesozoic fossils resembling Araucariaceae were interpreted by Knapp (2007) as evidence that *Agathis* trees survived the Oligocene drowning. However, more recent research (Biffin et al. 2010) revealed the taxonomic placement of the fossils to be uncertain; relaxing the fossil-based assumptions in the *Agathis* phylogeny gave an age of 23 million years for the New Zealand *Agathis* lineage.

While many different aspects of biogeography have been studied worldwide, New Zealand (NZ) biogeography, in particular, tends to focus on discussing vicariance and dispersal in the history of NZ's biota. Although New Zealand only fully emerged circa 25 million years ago (mya), its origins are rooted in Gondwanaland, a supercontinent that was fully formed by ca. 500 mya, and began to break up ca. 185 mya (Veevers 2004). The land masses that were previously part of east Gondwanaland are Australia, Antarctica, and the microcontinent Zealandia. Zealandia separated from Antarctica and Australia approximately 85 mya, shortly before the latter two continents split (Yan & Kroenke 1993). By around 65 mya, the oceanic gap between the New Zealand region of Zealandia and Australia (including Tasmania) had grown to its current width of 1,500 km (Yan & Kroenke 1993). Today, most (approximately 93%) of Zealandia lies submerged; the emergent fraction includes NZ (which formed 25 mya; Graham 2008), New Caledonia, the Chatham Islands, and the Subantarctic Islands (Goldberg et al. 2008; Mortimer 2004; Neall & Trewick 2008; Wallis & Trewick 2009).

Dispersal versus vicariance in the history of New Zealand's fauna has become the subject of enormous debate over the past few decades. A major part of New Zealand's cultural identity is

the idea that it is an isolated country with unique biota that has been evolving on the New Zealand landmass since it split from Gondwana (BBC 2016; Meyer-Westfeld 2014). The commonly held concept that New Zealand's biota is ancient, long-isolated, and unique is often cited as common knowledge in popular literature (e.g. Bellamy et al. 1990; Meyer-Westfeld 2014). New Zealanders hold their native wildlife in close regard due to its high level of endemism, and associated feelings of uniqueness and an ancient origin. Evidence that dispersal may have played a major part in the origin of New Zealand wildlife has been met with mixed sentiment, and sometimes aggressive rebuttal (Biffin et al. 2010; Craw, Grehan & Heads 1999; Craw 1979; Hill et al. 2008; Knapp et al. 2007;. Lee, Bannister & Lindqvist 2007; Stöckler, Daniel & Lockhart 2002). For example, Craw's (1979) response to McDowall's (1978) critique of vicariance biogeography with "McDowall's arguments about the role of dispersal in biogeography lack coherency" and "McDowall's arguments about the falsifiability criterion simply reveal his basic commitment to a "logical positivist" philosophy of science". Though there is some evidence that vicariance has played a role in the history of some New Zealand species (particularly short-range endemics) (Boyer & Giribet 2009; Giribet & Boyer 2010; Toon et al. 2010), evidence for the majority of species dispersing to New Zealand from Australia within the last 25 million years continues to mount (Baker, Yu & DeSalle 1998; Chacón et al. 2012; Chapple, Ritchie & Daugherty 2009; Colloff & Cameron 2014; Goldberg et al. 2008; Mitchell et al. 2014; Renner, Strijk, Strasberg & Thébaud 2010; Steven A. Trewick & Gibb 2010; Steven A. Trewick et al. 2007; Vink & Paterson 2003). Most studies concerning dispersal versus vicariance in New Zealand biota have concentrated on a particular taxon (e.g. bats; Teeling et al. 2005, birds; Mitchell et al. 2014; Tennyson et al. 2010; Trewick & Gibb 2010; Worthy et al. 2010, or spiders; Vink & Paterson 2003). However, now that many individual case studies have been developed, drawing them together and looking at New Zealand biota as a whole will reveal more about the patterns and processes of New Zealand biogeography than looking at single groups alone. Clarifying the origin of New Zealand biota has strong implications for the national identity and culture of New Zealanders, as well as the nature of evolution and biogeography on oceanic islands.

3.1.1 Research aim and objectives/ research questions

The purpose of this review is to draw together biogeographical research, focused on New Zealand as it may be considered a microcosm for global biogeography (de Queiroz 2014; McDowall 2008). Using linear modelling, I will answer the following questions:

1. How did most of the taxa studied arrive in New Zealand? Since the most recent reviews have described an increasing trend in evidence for the importance of dispersal in the history of NZ's biota (Tennyson 2010; Trewick & Gibb 2010; Trewick et al. 2007), I predict that the majority of taxa studied will have been found to have dispersed to New Zealand (not necessarily independently) after Zealandia split from Gondwana.

2. Are taxa with a smaller range of suitable habitat types less likely to have dispersed across the Tasman Sea than species with a larger range of suitable habitat types? I expect that any taxa that do appear to be relicts (or "ghosts"; Gibbs 2006) of Gondwana are very restricted in the types of habitat in which they are able to survive.

3. Are more vagile taxa more likely to have dispersed than less vagile taxa? I hypothesise that taxa with a long history of vicariance have an overall lower ability to disperse long distances.

4. Are dispersal or vicariance conclusions by researchers associated with particular time periods or author regions? I hypothesise that there is no link between author region, or year, and conclusion.

3.2 Methods

The search engine Google Scholar was searched in March 2016 using the following terms: **species, biogeography, Zealand, Zealandia, OR Oligocene and Gondwana*.** The resulting set of articles was filtered so that only original research papers published between 2005 and 2016, and pertaining to living organisms as opposed to pure geology, were included in the analysis. Prior to 2005, the literature was generally more speculative and used less rigorous methods than those that have since been developed; for example, using tree topology only to infer biogeographical history (e.g. Ericson et al. 2002). Previous review papers have dealt with earlier New Zealand biogeographical literature (e.g. Goldberg, Trewick & Paterson 2008). Since articles are ordered by relevance in Google Scholar, less relevant articles were excluded from the analysis by only assessing the first 100 articles output by the search (after which the entries became less relevant, determined by individual inspection). Each article was examined to ensure that it was relevant to NZ biogeography, and to evaluate the strength of the evidence. Occasionally, articles were found with conclusions drawn based entirely upon circular reasoning (primarily those invoking panbiogeography as evidence). Circular reasoning is an argument which assumes that what it is trying to prove is already accepted as true. For example, panbiogeography arranges organism "tracks" (lines between current distributions) on a map based on the assumption that organisms have moved with the landmasses they inhabit. The patterns shown by the tracks cannot therefore be invoked as evidence for vicariance (McDowall 1978; Waters et al. 2013). Articles using circular reasoning were not included in the analysis, as the major focus of the analysis is to determine the proportion of evidence pointing towards dispersal versus vicariance. The following information was recorded from each article: [1] the general conclusion (e.g. all the subject lineages dispersed to NZ, or at least some lineages appear to have been in Zealandia since it broke from Gondwana) [2] the choice of taxon studied (bird, insect, lizard, onychophoran, crustacean, other arthropod, arachnid, mollusc, fish, angiosperm, bryophyte, gymnosperm), [3] the taxon's general dispersal ability (in this case, the

distance it is capable of travelling) within a lifetime (low <10 km, medium 10–100 km, high >100 km), [4] body weight during the life stage with the highest likelihood of dispersal, [5] body weight as an adult, and [6] whether the taxa studied were specialists (i.e. with strict habitat or food requirements) or generalists. A given taxon was considered a specialist if its known range is strictly within one ecosystem zone (Singers & Rogers 2014), or if its diet is known to be monophagous (contain only one species or genus). A taxon was considered a generalist if its known range covers more than one ecosystem zone, or its diet contains more than one genus. This niche-width designation is based on the realised Grinnellian niche concept (Devictor et al. 2010; Grinnell 1917), and focuses on the requirements of the organism rather than its effect on the environment. Ecosystem zones were classified based on Singers and Rogers (2014) (for terrestrial ecosystems) and the Coastal Biogeographic Regions Classification system (Ministry for the Environment 2013) (for marine ecosystems).

A random forest classification tree in R (Liaw & Wiener 2002) was used to determine how much error was explained by each variable. The variables that most explained the error were input into linear models in R (R Core Team 2013) using the packages LME4 and AICcmodavg. A complete general linear model was constructed with author's conclusion (dispersal or vicariance) as the response variable, and the following explanatory variables: taxon general type; taxon dispersal ability; taxon habitat type; and taxon food type. A set of models was created incorporating different combinations of variables, and model fit was assessed using the Akaike information criterion, corrected for small sample size (AICc).

3.3 Results

Out of the first 100 articles retrieved by the Google Scholar search engine, 40 were selected as suitable for analysis (see Appendix B for full list). The remaining articles were incomplete or in books or journals to which access was restricted (12), and/or were irrelevant (8), repetitions or analyses of previous studies which came to the same conclusions (7), reviews (15), and/or based on circular or flawed logic (21, e.g. those invoking panbiogeography alone to test for vicariance; Waters et al. 2013).

Authors in 16 papers (40%) concluded that their results showed at least one New Zealand lineage to have origins determined by vicariance. However, three vicariance conclusions (Rheindt et al. 2014; Wright et al. 2008; Lee et al. 2012) were drawn from data that suggest the lineage arrived in New Zealand after the split from Gondwana, but before the Oligocene Drowning. Since Zealandia had already split from the rest of Gondwana, and there was ocean between the two continents, these lineages must have dispersed over water to Zealandia from Gondwana (Gibbs 2006). Their distribution is, therefore, a result of both vicariance and ancient dispersal. The results of these studies indicate that these "Zealandian" lineages persisted in New Zealand through the Oligocene drowning. A further four studies had both data and author

conclusions agreeing on a Zealandian lineage history including ancient dispersal, vicariance, and survival of the Oligocene drowning. The remaining 20 papers (50%) reported recent dispersal to New Zealand within the last 20 million years.

The variables that most explained the variation in taxon history were the dispersal ability (24.1% mean standard error), publication year (23.5% mean standard error), taxon (21.6%) and food type (generalist or specialist) (21.1%) (Fig. 3.2). Habitat type (generalist or specialist) was excluded from linear modelling, as it explained almost no error.

Models are described in Table 3.1. AICc numbers decreased most when the variable taxon was removed from the model. The model with the lowest AICc included only dispersal ability as the explanatory variable; this was also the only model with a significant p-value for the explanatory variable ($p=<0.01$). None of the models had a good model fit according to McFadden's R-squared (0.2–0.4 indicates a very good fit; Lee 2013; Louviere, Hensher & Swait 2000). There was an apparent trend in dispersal ability: most of the taxa studied that had a high dispersal ability were reported to have a history of dispersal to New Zealand, and most of the taxa that had a low dispersal ability were found to have a history of vicariance (Fig. 3.3). Taxa with a medium dispersal ability were predominantly found to have dispersed to New Zealand. However, this trend is weakly supported (McFadden's pseudo R-squared=0.032).

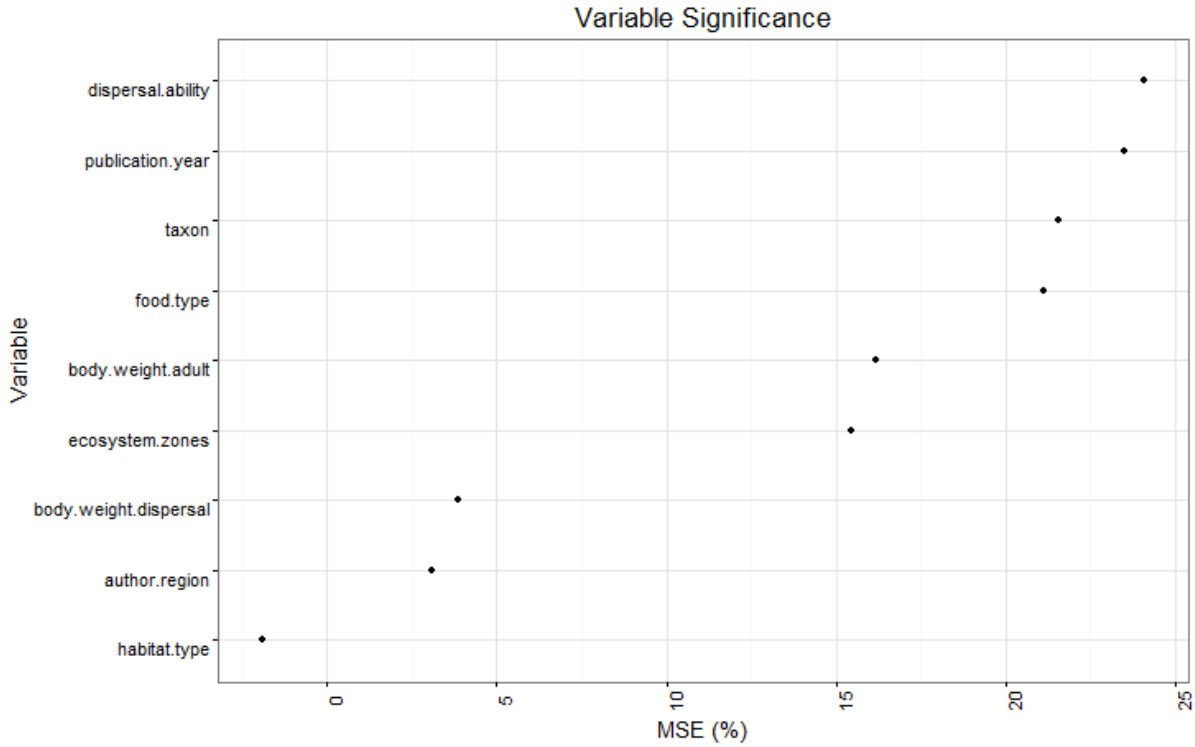

Figure 3.3: The percentage mean standard error explained by different variables tested using the random forest.

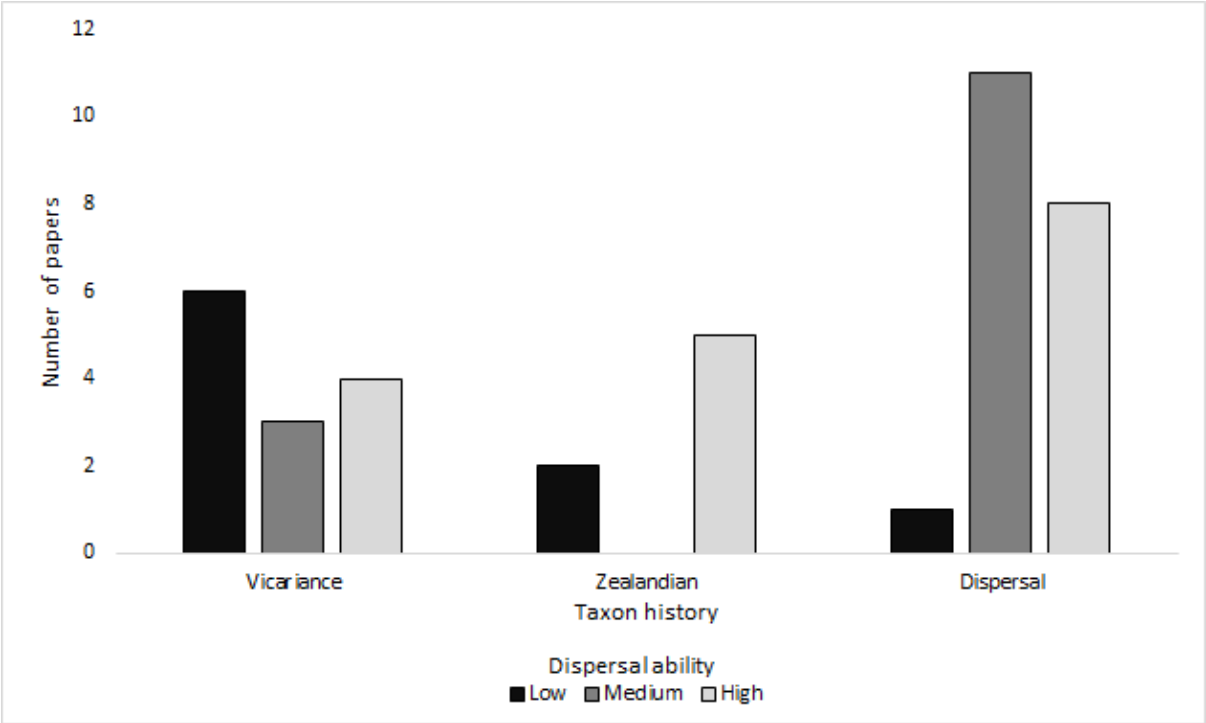

Figure 3.2: Bar graph illustrating the number of papers reporting vicariance, dispersal, or pre-Oligocene dispersal (Zealandian) history. Black bars represent taxa with a low dispersal ability <10 km in a lifetime); dark grey bars indicate taxa with a medium dispersal ability (10–100 km in a lifetime); light grey bars represent taxa with a high dispersal ability (>100 km in a lifetime).

Table 3.1: Models describing the effect of the chosen explanatory variables on a taxon's history of dispersal versus vicariance. All p-values were >0.05 except where marked by an asterisk *. Two asterisks ** indicate p<0.01.

Model number	Explanatory variables included	AICc	R-squared (McFadden's)
1	Dispersal ability Publication year Taxon Food type Adult body weight Ecosystem zones Body weight dispersal Author region	144.9	0.118
2	Dispersal ability Publication year Taxon Food type Adult body weight Ecosystem zones Body weight dispersal	144.46	0.105
3	Dispersal ability Publication year Taxon Food type Adult body weight Ecosystem zones	142.75	0.102
4	Dispersal ability Publication year Taxon Food type Adult body weight	141.34	0.097
5	Dispersal ability Publication year Taxon Food type	139.37	0.097
6	Dispersal ability Publication year Taxon	137.46	0.096
7	Dispersal ability Publication year	118.55	0.034
8	Dispersal ability**	116.78	0.032
9	Dispersal ability Publication year Taxon Food type Adult body weight Ecosystem zones Body weight dispersal Author region	123.88	0.075
10	Taxon	134.22	0.072

3.4 Discussion

The research presented in this chapter shows that dispersal ability, habitat or diet specialisation, taxon type, and body size do not explain the variation found in the biogeographical history (i.e. dispersal or vicariance) of New Zealand's biota. Further, the variation is not explained by any correlation with publication date or the region where the first author is located. There is a weakly supported correlation between dispersal ability and biogeographical history.

The results from this study are surprising: there was no strong correlation found between biogeographical history and any of the major factors expected to contribute to dispersal or colonisation ability. Some variables (e.g. dispersal ability) could be identified as explaining more of the variation than others (Fig. 3.2), but none of the variables explained more than 25% of the variation, and none of them showed a strong relationship with the response variable (Table 3.1). Dispersal ability was identified as significant when modelled on its own (Model 8), so may have a weak relationship with biogeographical history of taxa. Taxon type, food type, adult or dispersal stage body weight had no apparent relationship with the response variable. Effect sizes varied, but all were too low to be considered to have a genuine effect on dispersal or vicariance in an organism's history. Variables included to test for confounding factors associated with author bias were publication year and author region, neither of which had a significant effect or high effect size when modelled against the response variable. Model 8 had the lowest AICc number of all the models, partially because it only contained one explanatory variable, but the AICc number of Model 8 was also lower than that of Model 10, which also contained only one explanatory variable (Taxon). The lowest AICc value indicates that Model 8 was the model that explained the most of the variance with the least number of variables (Hurvich & Tsai 1993). However, the McFadden's pseudo R-squared value was not highest for Model 8, indicating that it did not show the strongest trend.

On the other hand, Figure 3.3 shows that more taxa were reported to have a history of vicariance when they were known to be poor dispersers. More taxa were reported to have dispersed from Australia within the last 25 million years when they were known to have a high dispersal ability. These two trends are as expected; highly vagile species should be able to disperse frequently and easily over long distances, while non-vagile species should only be able to disperse long distances under highly unusual circumstances, such as by rafting. However, the trends shown in Figure 3.3 are not significant: the explanatory variables involved do not have a significant effect on the response variable, and their inclusion in a model does not increase its explanatory power. Further, models with the variables shown in Figure 3.3 have low r-squared values (Table 3.1). Figure 3.3 may simply illustrate noise, as an artefact of small sample size. Alternatively, with a larger sample size, a stronger trend may be seen correlating dispersal ability with biogeographical history. The weak trend shown in Figure 3.3 may also illustrate recent signal; while 33% of studies included in this analysis showed strong evidence for vicariance over dispersal, this percentage may decrease over evolutionary time as more

species disperse from Australia to New Zealand. Unlike ancient vicariance, dispersal is an ongoing process: There are likely to be more opportunities for less vagile species to disperse over the Tasman Sea in the future, leading to a decrease in the percentage of species that arrived in New Zealand by vicariance. However, the fact that the majority of dispersal papers dated the dispersal to within 10 million years of the rise of New Zealand suggests that colonisation by dispersal may become more difficult with time, as New Zealand's biota and ecosystems became established. Further, the habitat and biota of New Zealand has changed since its emergence; many species are likely to have gone extinct, leading to a high probability that the number of lineages which have arrived in New Zealand by any means will be underestimated.

Recent reviews of evidence for dispersal versus vicariance in New Zealand have concluded that the majority of New Zealand biota arrived there by trans-oceanic dispersal (e.g. Giribet & Boyer 2010; Trewick et al. 2007; Waters & Craw 2006). There has even been speculation that the entire biota originated by dispersal, and that there may have been no emergent land during the Oligocene drowning period (Landis et al. 2008). However, the papers considered in this review demonstrate that there is evidence for biota surviving the Oligocene drowning (e.g. Beu, Marshall & Reay 2014; Boyer & Giribet 2009; Lee et al. 2012; Toon et al. 2010; Worthy et al. 2006). While the majority of papers find evidence for dispersal, "ghosts of Gondwana" are still occasionally found. The current debate over whether New Zealand's biota show ancient vicariance or recent dispersal is irrelevant: it appears to be neither one nor the other, but a mixture of both. Judging by the evidence, the majority of biota arrived in New Zealand by dispersing there from Australia within the last 25 million years, but there was still sufficient land during the Oligocene drowning to support those who had dispersed to New Zealand before the Oligocene, and those who had survived on Zealandia since it split from Gondwana.

The research presented in this thesis provides sufficient evidence to question biological interpretations of species biogeographical histories: for example, their habitat restrictions, or diet specialisation. While biological factors might aid speculation as to the method of dispersal a taxon may have used, such factors do not appear to have a strong effect on the ultimate conclusion as to the biogeographical history of a taxon. Future reviews may find a strong correlation between dispersal ability and biogeographical history, but this study does not provide evidence that the correlation is strong enough to be considered important. These findings are contrary to suggestions in the literature that particular taxa may be predisposed towards vicariance due to habitat constraints (e.g. Crisp et al. 2011; Toon et al. 2010).

In three of the 40 papers (D. E. Lee et al. 2012; Rheindt et al. 2014; T. F. Wright et al. 2008), authors concluded that at least some New Zealand taxa showed a vicariant biogeographical history; however, their results only showed that the taxa had been present in New Zealand before the Oligocene drowning, and not since the breakup of Gondwana. Therefore, these taxa probably dispersed to Zealandia prior to the Oligocene, and survived the Oligocene drowning.

Alternatively, some lineages may have arrived in New Zealand after the Oligocene, but their closest relatives in Australia have since become extinct. Divergence from their closest extant relative would therefore be earlier than the date that the lineage left Australia. Lineage extinction can complicate biogeographical hypotheses, especially given the paucity in the fossil record.

Methods used to infer vicariance or dispersal vary considerably, and many of the studies assessed for inclusion in this study were discarded due to invoking panbiogeography, distribution, or St Bathans Fauna fossils as the sole evidence for vicariance. With the advent of molecular methods, panbiogeography is decreasing in popularity as a biogeographic tool; however, it is still occasionally used (Waters et al. 2013). Panbiogeography involves drawing lines between current distributions of particular taxa of interest. These lines (called tracks) are used to infer the geological processes leading to the current distribution of taxa. However, modern understanding of the frequency of dispersal, even amongst non-vagile species, renders panbiogeography unsuitable as the sole tool for assessing the biogeographical history of organisms (de Queiroz 2014; Waters et al. 2013), as it does not consider dispersal. Distribution of organisms cannot be used as a sole indicator of dispersal or vicariance, as shown by the numerous studies that have found evidence for dispersal in organisms with a Gondwanan distribution (e.g. *Nothofagus*; Craw 1985; Knapp et al. 2005).

The St Bathans fauna contains fossils of a maximum of 19 million years in age and are numerous and highly diverse. Presence of a lineage in this fauna is often considered evidence that those lineages have been in Zealandia since it split from the rest of Gondwana (e.g. Worthy et al. 2010; Worthy et al. 2011). However, at the time that these fossils formed, New Zealand had been emergent for at least several million years, giving time for species to arrive and colonise the new island. While the diversity and number of lineages may appear to imply that they must have been on New Zealand for many millions of years, the evidence from St Bathans Fauna does not prove that all the lineages survived ancient vicariance or even the Oligocene drowning. Many isolated islands of recent origin have very large numbers of lineages that have colonised in a short time (e.g. Chatham Islands; Heenan et al. 2010). Presence of a lineage on a new island does not, therefore, indicate that it has been there for a long time. The large and early influx of lineages may also be explained by a large dispersal event, such as a rafting island of debris. Many species may have found colonising the new island easy in the absence of competition or predators, which enables them to expand their niche breadth and become more abundant (ecological release; Bolnick et al. 2010; Cox & Ricklefs 1977; Mesquita, Colli & Vitt 2007). An alternative theory is that the lineages shown by the fossils could have gone extinct during the period of inundation, and subsequently recolonised (as *Agathis* appears to have done; Biffin et al. 2010). Some lineages present in the St Bathans fauna have gone extinct (Worthy et al. 2006 2010; Worthy et al. 2009; Worthy et al. 2011). However, since St Bathans Fauna fossils represent many lineages known to exist recently in New Zealand (e.g. moa;

Tennyson et al. 2010 and tuatara; Jones et al. 2009), the most parsimonious explanation would be for those fossils to be the ancestors of the current lineages. The Clarence Valley mid-cretaceous fossils, however, show organisms present in Zealandia before the Oligocene drowning, some of which still exist today (e.g. Beu et al. 2014). These organisms may have survived the Oligocene drowning, or become extinct and recolonised. Such fossils are therefore of limited use in vicariance testing.

Molecular evidence in the form of dated phylogenies can be considered one of the most robust modern methods of vicariance testing (Crisp et al. 2011; de Queiroz 2014; Trewick et al. 2007). However, dated phylogenies can also vary in the standard to which they are implemented and interpreted. For example, missing (unsampled) lineages within a clade, or removing them from the phylogeny ("pruning"), can give an impression that the common ancestor of species in New Zealand and Australia included in the phylogeny are older than they are (Goldberg, Trewick & Powlesland 2011). Extinctions also remove lineages from trees, but the result of some extinctions (including the New Zealand Oligocene extinctions) could be trees with shallow but diverse crown lineages. Dating the beginning of radiant diversification within these phylogenies may underestimate their ages (Sharma & Wheeler 2013); dating divergence from the allopatric sister group of the lineage is more conducive to getting a result that does not underestimate the age of the lineage.

The reasoning behind conclusions based on dated phylogenies may not consider their limitations. For example, a lineage may have begun to diversify before dispersal. Alternatively, a lineage may disperse to a different landmass (e.g. Tasmania) and later disperse from there to the landmass on which it currently resides (e.g. New Zealand). If the lineage on the previous landmass (Tasmania) subsequently goes extinct, then the current lineage may appear to have arrived on its current landmass long before it actually did arrive. The date that a lineage arrived on a particular landmass cannot therefore be ascertained precisely, but can only be inferred from divergence dates. There is also a time lag of indeterminable length between divergence from the most recent common ancestor (due to dispersal) and arrival on a new land mass. This limitation must always be taken into consideration when interpreting phylogenies.

A further limitation of phylogenies can be the method used to date them. Substitution rates can vary greatly between closely related lineages (Janecka, Chowdhary & Murphy 2012), and must be interpreted as imprecise if substitution rates are used to date phylogenies of organisms that are not closely related to the organism from which the substitution rate was calculated. Fossil and geological dates are also used to date divergences, though they too can be prone to error (Graur & Martin 2004; Ho & Phillips 2009; Marshall, Wiens & Whitlock 2008; Parham et al. 2011; Pulquério & Nichols 2007; Ronquist et al. 2012).

Dispersal, vicariance, and ancient dispersal with subsequent survival of the Oligocene drowning are the three major possible biogeographic histories used to describe New Zealand biota.

However, when investigating which history pertains to a particular taxon, knowing which null hypothesis to use is sometimes difficult. Historically, vicariance was hypothesised as the origin of most biota, and was used as the null hypothesis when searching for exceptions (Perrie & Brownsey 2007; Sanmartín & Ronquist 2004; Wolf, Schneider & Ranker 2001). However, Landis et. al. (2008) proposed that dispersal should be the null hypothesis, due to the lack of geological evidence for continuous tracts of emergent land during the Oligocene drowning. Recent evidence showing that some terrestrial species are likely to have survived the Oligocene drowning (e.g. Giribet & Boyer 2010) indicate that there was emergent land throughout the Oligocene, raising vicariance as a possible biogeographic history once again. However, the majority of studies show taxa that, according to the evidence presented, appear to have dispersed to New Zealand. Since the majority of taxa appear to have dispersed, dispersal is still a valid null hypothesis in most cases. The confusion regarding which null hypothesis to use may explain some of the frequency with which taxa are tested more than once, sometimes with differing results. For example, Wright et. al. (2008) assumed that dispersal was relatively rare in parrots, and that they were more likely to move with the landmasses they inhabited. Thus, they rejected their fossil-based phylogeny and concluded that New Zealand parrots had remained on Zealandia since it split from Gondwana. However, Rheindt et. al. (2014) took recent evidence for the high frequency of dispersal into account and concluded that New Zealand parrots had undergone ancient dispersal. The parrot studies also illustrate how geological dates have limited application to vicariance testing, as the degree to which they influenced divergence within the phylogeny is uncertain. The biogeographic histories of particular New Zealand taxa are often studied more than once, with different evidence leading to different conclusions (e.g. the *Agathis* argument; Biffin et al. 2010; Hill et al. 2008; Knapp et al. 2007; Lee et al. 2007; Stöckler et al. 2002).

Based on the outcome of the research presented in this chapter, I recommend that the biology of an organism (e.g. its habitat requirements or dispersal ability) cannot be relied upon as evidence towards its biogeographic history. Despite the limited range of taxa that have thus far been studied with respect to New Zealand biogeography, a wide variety of life histories has been covered. The taxa covered in this chapter may therefore be considered a microcosm of New Zealand taxa, and the findings presented here probably reflect broader patterns of biogeography in organisms with similar life histories that have not yet been studied. Further research needs to be conducted into the effects of dispersal ability on geographic distribution, perhaps with a worldwide focus and a greater sample size. However, dispersal ability is not strongly supported as connected to biogeographic history in the current study. It is possible that dispersal ability affects the biogeographic history of the biota of oceanic islands that split from other landmasses recently. However, over evolutionary and geological time, the number of opportunities for trans-oceanic dispersal increases, and dispersal ability becomes less of an indicator of biogeographic history. The focal taxon of this thesis, *Cantuaria*, is an example of a lineage that appears to have undergone trans-oceanic dispersal approximately 18 million years

ago (see Chapter 5), but the Southern Alps which formed 8–5 mya appear to be a recent barrier to gene flow between eastern and western South Island species. Thus, a dispersal-limited lineage may initially be prevented from dispersing over a barrier, but over evolutionary time dispersal becomes more likely. Ecosystem and food types are unreliable determinants of biogeographic history, possibly because of the ability of organisms to adapt to different food types. However, food specialisation that is connected to other aspects of an organism's ecology may delay dispersal and colonisation of new landmasses. Braby et. al. (2005) used food specialisation as a possible explanation as to why troidine butterflies have colonised Madagascar but not Africa. The tribe Troidini feed only on poisonous pipevine plants, predominantly of the *Aristolochia* genus; as a result, the larvae are toxic (Sime, Feeny & Haribal 2000). However, closely related species within the family Papilionidae feed on a variety of plant genera, and Troidini may be able to adapt to feeding on African plants. Since its predator defense strategy is closely dependent on its diet, however, such adaptation and colonisation may take longer than if it relied on other anti-predator mechanisms. Alternatively, food plants within *Aristolochia* may be able to colonise Africa, enabling the Troidini to follow suit. A species' biology may restrict its ability to disperse long distances in the short term. However, over long periods of time, the biology of the species matters less as unusual events may produce conditions conducive to the dispersal and colonisation of even highly habitat-specific species. For example, the spur-winged plover (*Vanellus miles* Bodaert, 1783), silvereye (*Zosterops lateralis* Latham, 1801), white-faced heron (*Ardea novaehollandiae* Latham 1790), royal spoonbill (*Platalea regia* Gould, 1838), and welcome swallow (*Hirundo tahitica* Gould, 1842) only began to colonise New Zealand after anthropogenic land-use changes created the open habitat that they require (Hobbs, 2000). Their biology had previously prevented their colonisation of New Zealand, but changes in the environment enabled their colonisation (Hobbs, 2000). Future environmental changes, including further habitat loss, or climate change, could conceivably facilitate more colonisations, for example of species currently restricted to warmer regions of Australia.

The current study supports recent trends towards using dispersal as a null hypothesis when considering New Zealand fauna, initiated by Landis et. al. (2008). Worldwide fauna may show different tendencies towards dispersal or vicariance, but dispersal is possible over evolutionary and geological time, even when large areas of ocean must be crossed, such as the Tasman Sea. Current understanding of New Zealand biota as ancient and isolated for 80 million years (perpetuated by media; BBC 2016; Meyer-Westfeld 2014) is a popular idea, as it maintains the image of New Zealand's iconic wildlife as unique and interesting. The fact that most biota appears to have dispersed to New Zealand within the last 25 million years does not make it less unique or interesting. New Zealand supports one of the highest levels of endemicity on Earth (Gibbs 2006); its flora and fauna have adapted to the wide range of environments present in New Zealand, diverging and speciating during their dispersal. Most biota that have been studied have been evolving in New Zealand for at least ten million years, and are, therefore, still closely

tied to New Zealand history and geology. The fact that invasive mammals have such a detrimental effect on New Zealand wildlife (Craig et al. 2000; Norton 2009) is testament to the high degree to which New Zealand biota has adapted in order to live there prior to human colonisation, and the subsequent uniqueness of New Zealand's biota.

The research presented in this thesis focuses on the biogeography of a taxon (*Cantuaria*) which has previously been assumed to have been on Zealandia for 80 million years (Irish 2001). *Cantuaria* is similar to other species assumed to have a history dominated by vicariance, in that it is dispersal-limited, and endemic. Chapter 5 reveals that, like many other dispersal-limited endemics (Chapple et al. 2009; Cooper et al. 2001; Mitchell et al. 2014), *Cantuaria* appears to have dispersed to New Zealand after the Oligocene drowning.

In conclusion, over evolutionary and geological time, the process of dispersal can affect all biota: even highly specialised taxa with particular habitat and food requirements. New Zealand's biota shows a variety of biogeographical histories, with most lineages having dispersed from Australia within the last 25 million years. There is evidence for emergent land during the Oligocene drowning period, upon which a few lineages survived. However, author bias or misinterpretation of evidence can sometimes lead to conclusions that do not fully represent the evidence presented. There is not a simple line to be drawn between dispersal or vicariance; some lineages have dispersed over a short distance to Zealandia before it was in its current position, and survived the Oligocene drowning. New Zealand is an excellent microcosm for understanding global biogeography, as it is sufficiently isolated to test the ability of lineages to disperse, but was also able to accommodate lineages surviving on Zealandia since it split from Gondwana. Future research should continue to test the biogeographical origins of biota to increase our understanding of vicariance, dispersal and colonisation.

Chapter 4
Beetling: a method for catching trapdoor spiders (Idiopidae) using tethered beetles

Published as a journal article (Smith, V. R., Vink, C. J., Cruickshank, R. H. & Paterson, A. M. (2015). Beetling: a method for capturing trapdoor spiders (Idiopidae) using tethered beetles. *Arachnology*, *16*(8), 294–297. https://doi.org/10.13156/arac.2015.16.8.294)

4.1 Introduction

Trapdoor spiders (Mygalomorphae: Idiopidae) are widespread in the southern hemisphere (Platnick 2014), and almost entirely occupy a fossorial niche. Idiopids dig underground burrows up to 49 cm deep (Irish 2001) from which they may never fully emerge. Their high site-fidelity and low dispersal ability make Idiopidae particularly interesting from an ecological and evolutionary perspective (Bond & Stockman 2008; Cooper et al. 2011), although their nocturnal, burrow-dwelling, life histories make collecting samples difficult.

Commonly used methods of collecting idiopids include digging (Irish 2001; Marples & Marples 1972), and pitfall-trapping for males (Engelbrecht 2013) and nematode-infected females (Poinar Jr & Early 1990). While often successful, these methods have obvious drawbacks. Idiopid burrows are usually deep, often in hard soil, and become convoluted around rocks and tree roots, making digging laborious and difficult, and damaging to the burrow and surrounding area. Digging can also result in the accidental dismembering of the specimen. Pitfall-trapping male Idiopidae can be successful when they are searching for females at specific times during the year. For example, male *Cantuaria* often leave their burrows in autumn and winter to look for females (Irish 2001), whereas female idiopids typically never leave their burrows (Engelbrecht 2013). Thus pitfall trapping is highly seasonal and is only suitable for the collection of male Idiopidae. The males collected using pitfall-traps may be immigrants and therefore pitfall-trapping a male does not enable reliable determination of the source population, as males may wander far from their source population in search of females. Both pitfall trapping and digging require carrying bulky and sometimes heavy equipment (shovels or pitfall traps), and trapping often requires multiple visits to a location at least a week apart.

Methods of trapping predatory vertebrates sometimes involve using live bait; for example, Falconiformes (birds of prey) may be trapped using a live prey species, such as a mouse or bird, inside a bal-chatri trap (a cage covered with nooses) (Berger & Mueller 1959; Dykstra et al. 2012). Food bait is often used to attract invertebrates for collection (for example, baiting pitfall traps with squid (Seldon & Beggs 2010), but few published studies have used live bait. Burrowing arachnids have been trapped using a specially designed container, the efficacy of

which may be increased by adding a live insect bait inside a vial (Henschel 1991), however, the success of this method relies on the individual leaving its burrow to encounter the trap.

I describe a new method for capturing trapdoor spiders called "beetling": the use of tethered mealworm beetles *Tenebrio molitor* Linnaeus, 1758 to attract female trapdoor spiders, in this case of the genus *Cantuaria*, to exit their burrows for easy collection. *Cantuaria* is a particularly speciose genus (42 currently recognised species) that is endemic to New Zealand, and exhibits typical idiopid habitat selection, preferring clay banks or damp forests. Our method is simple to execute, requires minimal equipment, and is successful when used to capture *Cantuaria* spp. While digging out a trapdoor spider usually takes about 20 minutes (pers. obs; M. Wakelin pers. comm.), and pitfall traps must be left out for at least a few days, a spider may be attracted instantly using a tethered beetle. Beetling was successfully used over three months to collect *Cantuaria* spp. from populations around New Zealand.

4.2 Methods

4.2.1 Beetles

Tenebrio molitor beetles were obtained from an existing culture in the Department of Ecology at Lincoln University, New Zealand. Mealworms (*T. molitor* larvae) are easily obtained from pet shops and animal feed suppliers in many countries. The beetles were maintained on a porridge oat substrate, with occasional pieces of bread, carrot, broccoli, dry meat or dog biscuit added to the substrate for extra nutrition. Beetles, larvae, and pupae were kept separate to avoid cannibalism.

Before use in the field, a single beetle would be selected based on size (smaller beetles for smaller species of *Cantuaria*) and tethered by passing one loop of cotton thread around the joint between the thorax and abdomen and behind the first pair of legs, if the beetle was needed immediately and was handled particularly carefully (Fig. 4.1a). A single loop was also used with other invertebrates, such as amphipods, that do not have narrow joints between body segments (Fig. 4.1b). Alternatively, one loop between the head and thorax, and another loop between the thorax and abdomen, could be used (Fig. 4.2). Using two loops of thread, rather than one, enabled greater control over the beetle, was less likely to cause damage, and prevented the beetle from escaping. The easiest way to get the thread around the beetle was to hold it by the abdomen and pass a loop of thread, tied with a single overhand knot, over the beetle's head. The knot can be tightened behind the pronotum, then pass the thread behind the front legs (which the beetle will lift if the abdomen is tilted back), crossed over and tied with two overhand knots behind the thorax (Fig. 4.2). The beetle can be tethered to a post or stick in the ground until needed, but care must be taken not to place it near spider burrows. After the same beetle was used for three consecutive nights, its tether was removed and it was returned to the source culture.

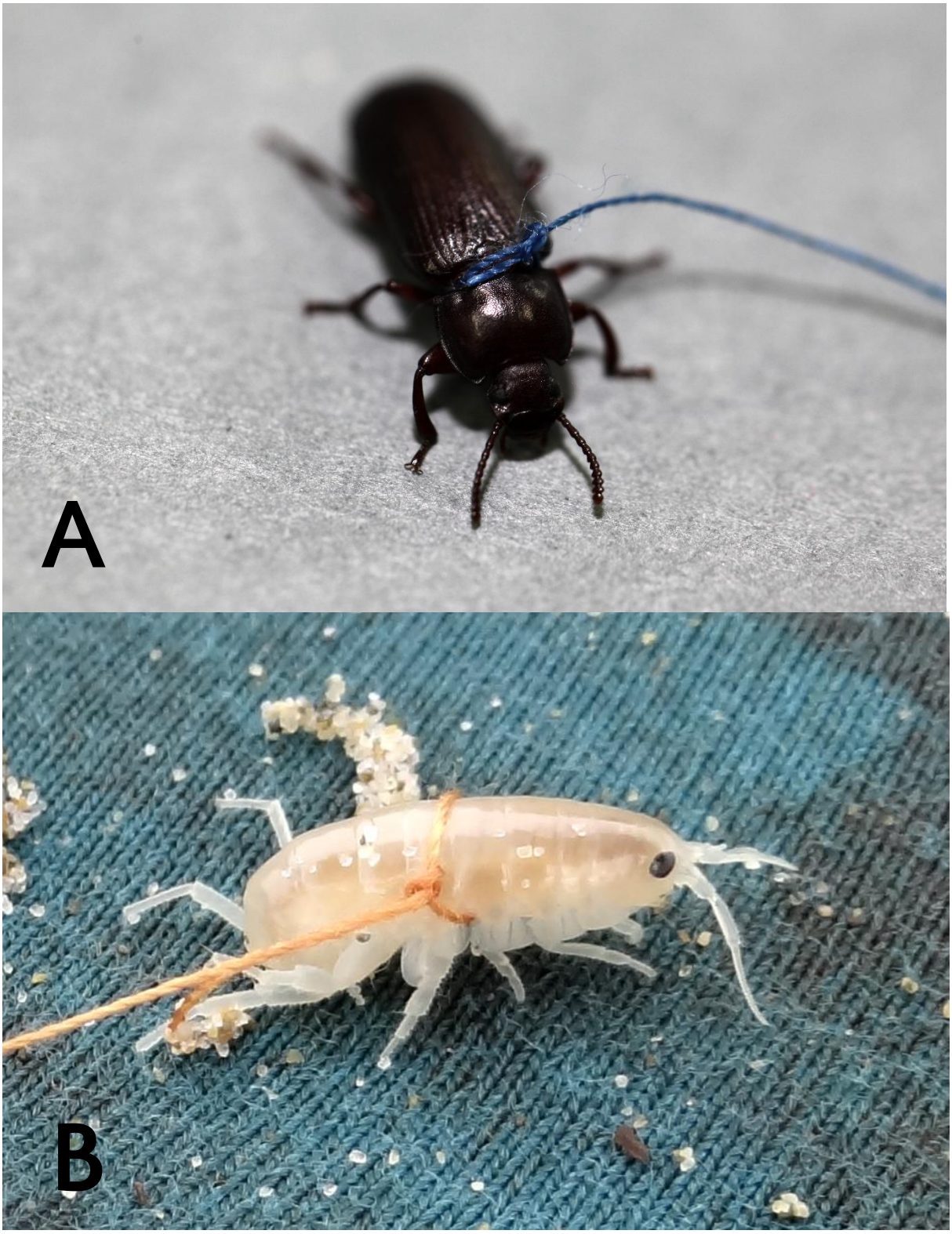

Figure 4.1: a *Tenebrio molitor* beetle (A) and an amphipod (B) (Talitridae Rafinesque, 1815) tethered with one loop of cotton thread.

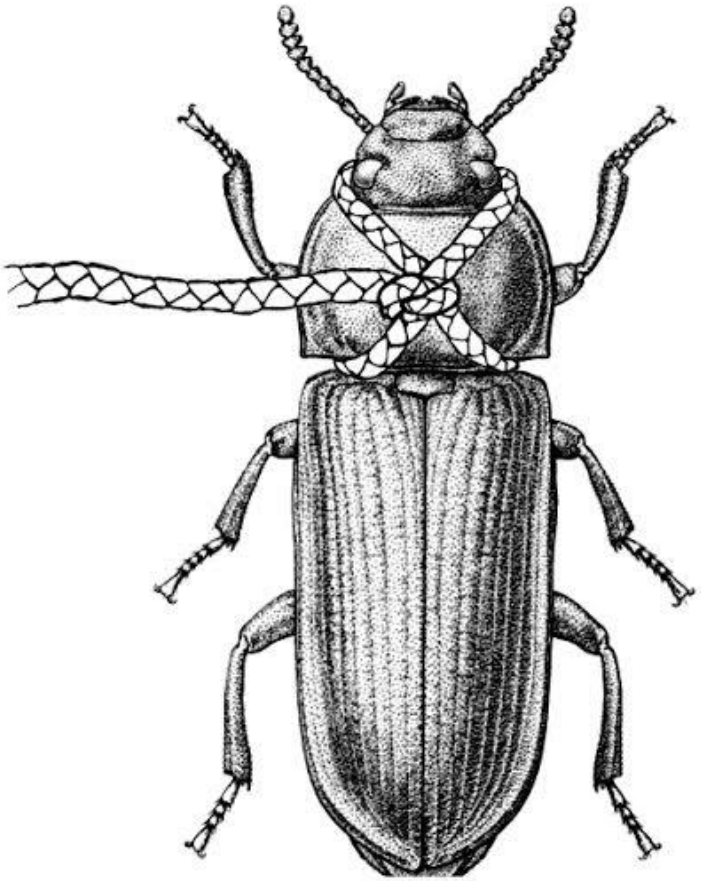

Figure 4.2: A beetle wearing a two-looped harness. Artwork by Alex Wooton (Canterbury Museum).

4.2.2 Identifying burrows

Cantuaria were sampled from Southland, West Coast, Otago, Canterbury, Nelson, Tasman, Wellington, and Manawatu-Whanganui regions in New Zealand (Fig. 4.4). Populations were located using local knowledge, and records from Forster and Wilton (1968) and Irish (2001). Burrows were identified and marked with popsicle sticks painted with red Dulux Spraypak™ Dazzle fluorescent paint. I aimed to locate and mark at least seven burrows per population; from these seven burrows, at least three specimens could usually be caught.

4.2.3 Attracting a spider

The beetle was placed adjacent to the lid or mouth of a selected spider burrow, with the thread kept loose to enable movement. If the beetle strayed too far from the lid, or appeared to be about to walk onto the lid itself, a quick tug on the thread would pull the beetle away from the substrate. If the thread was tugged too slowly or held taut, the beetle would grip onto the substrate, which could result in too much disturbance, and discourage the spider from leaving its burrow.

4.2.4 Collecting

If beetling was successful, the spider would leave the burrow to strike. At this point, the handler would remove the beetle and immediately drive a trowel into the ground between the spider and its burrow to block the entrance. Care was taken to point the trowel down the burrow, rather than across it, to avoid mutilating the specimen. If the trowel was inserted quickly enough, the spider would stop moving.

4.3 Results

4.3.1 Collecting success

Between December 2013 and November 2014, 130 *Cantuaria* specimens were collected from 102 populations located throughout the South Island and lower North Island of New Zealand (see Fig. 4.4). Beetling was conducted as far south as Stewart Island, and as far north as Makirikiri (near Whanganui) (see Fig. 4.4). Beetling was only attempted in the months of December, March, April, May, June, September, and November. Efforts were not evenly distributed throughout these months; in March, April, May, and June, collection was attempted approximately every night, whereas in December, September, and November, only the occasional collection was attempted. Beetling was always attempted first, and was used successfully to collect 123 individuals. If beetling proved unsuccessful in a population, digging would be attempted. In four populations, beetling failed to retrieve a spider, so individuals (n=7) had to be collected by digging or using a carabid beetle. On two occasions, beetling worked for some individuals but not others, and on six occasions no specimens were retrieved; the spiders were not attracted to the beetle, and the ground was too hard for digging.

Beetling also lured other fossorial invertebrates from their holes, including tiger beetle larvae (Carabidae), wolf spiders (Lycosidae), other Mygalomorphae (Hexathelidae, Nemesiidae) and vagrant spiders (Zoropsidae).

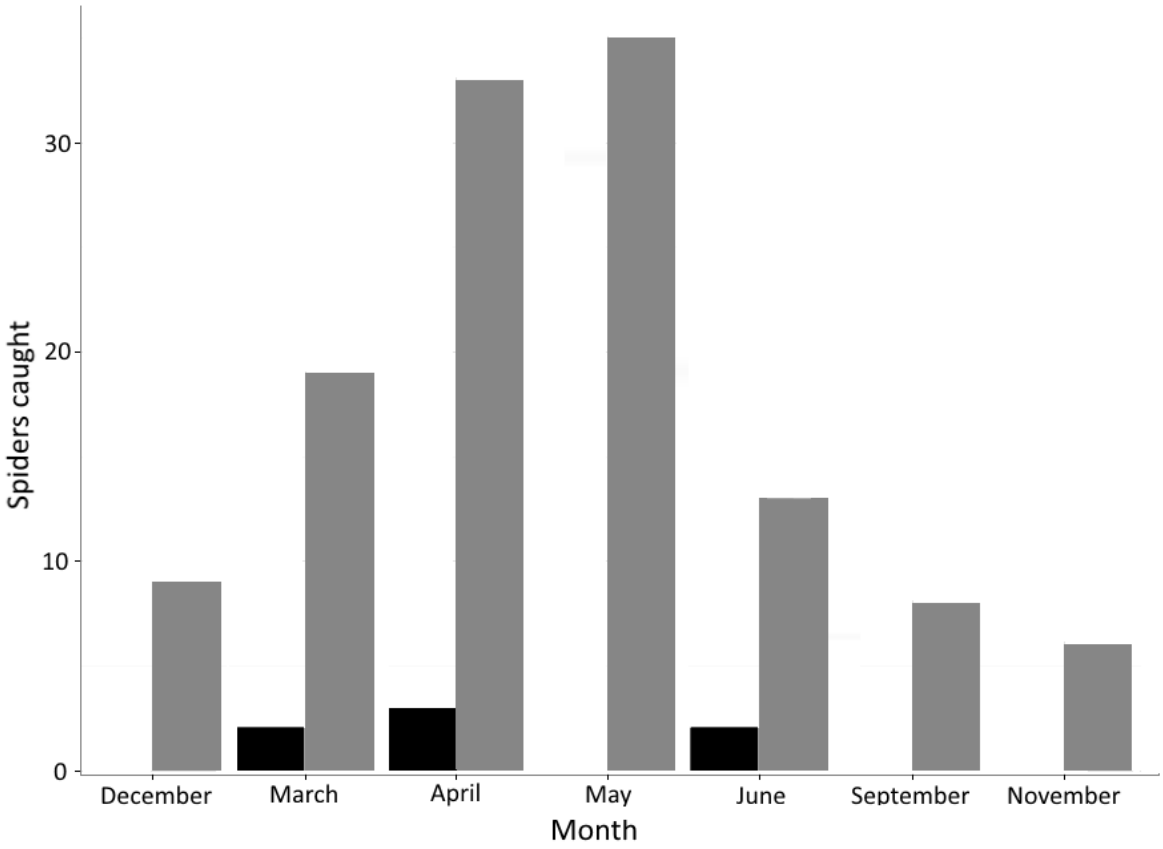

Figure 4.3: The total number of spiders caught per month, at all localities, when beetling was attempted. Grey bars show the number of spiders caught using beetling, and black bars show the number of spiders caught using another method after beetling had failed. Collecting effort was unevenly distributed between months. Graph constructed in R (R Core Team 2013) using ggplot2 (Wickham 2009).

4.4 Discussion

4.4.1 Beetle positioning

The following observations are offered as a guide to beetle positioning:

- Trapdoor burrows are surrounded by radial strands of silk (Irish 2001). If the beetle stands on one or more adjacent radial strands then the spider may strike immediately.

- Allowing the beetle to walk once over the lid of the burrow appears to alert an otherwise unresponsive spider.

- Pulling hard on the leash will cause the beetle to rear up, grasping at the substrate with its tarsi and causing more disturbance than leaving the leash slack and allowing the beetle to roam more freely. Varying the tautness of the leash (and therefore the amount that the beetle is pulling on the substrate) may entice an otherwise unresponsive spider.

- The most successful beetle position appears to be with its head approximately 2 mm from the front of the lid, and the leash tight so that the beetle is attempting to claw its way towards the entrance, but is not gaining any headway.

- If the beetle must be repositioned, snapping it quickly up prevents it from dislodging a large amount of substrate and disturbing the spider.

4.4.2 Waiting time

Occasionally, spiders were found with their tarsi outside the entrance to the burrow. Any movement around the burrow by the beetle handler would result in the spider withdrawing its tarsi. However, if the beetle could be lowered to the ground next to a tarsus, the spider would usually strike within approximately ten seconds. Other times between beetle deployment and spider strike were highly variable, but usually a spider would strike within ten minutes. Spiders took longer to strike if the beetle moved more slowly, or if the researcher's movements disturbed the spider.

Some *Cantuaria* reacted to the beetle defensively, by pulling their trapdoor lids inwards. Defensive *Cantuaria* were easily caught by thrusting the trowel into the ground just as the trapdoor was pulled in, while the spider was still near the lid.

4.4.3 Alternative methods of collecting trapdoor spiders

Repeatedly dragging a piece of grass past the burrow's entrance, as commonly used to lure burrowing spiders such as theraphosids (D. E. Hamilton 2008), often caused the spider to half-leave the burrow and strike, although the spider would not leave the burrow for long enough to facilitate capture. Carabid beetles *Megadromus antarcticus* Chaudoir 1865 and *M. guerinii* Chaudoir 1865 were also harnessed and deployed down burrows to chase the inhabitant out; carabids are highly aggressive, and often larger than the spiders. Tethered carabids were excellent at causing *Stanwellia kaituna* Forster 1968 to leave their burrows, but success was limited with *Cantuaria* spp., and often resulted in an injury to the spider. On one occasion, the carabid used its jaws to pull a female from its burrow. When deployed down a neighbouring burrow, however, the same carabid was eaten by a mother spider, possibly in defence of her spiderlings.

4.4.4 Limitations of beetling

On cold nights, *T. molitor* would often move too slowly to be attractive to *Cantuaria*. Warming the beetle with the researcher's body heat would temporarily encourage faster movement. Occasionally, beetles would stop and eat or drink from the substrate rather than moving; stationary beetles did not attract *Cantuaria*. Tethering the beetle on the ground enables it to take moisture and minerals from the soil prior to commencing beetling, reducing its tendency to stop moving.

Driving the trowel into the ground as the spider emerges from its burrow can sometimes result in mutilation of the specimen, particularly if it is large. Care must be taken to drive the trowel in the same direction as the burrow, rather than across it, to avoid damaging the specimen. In particularly hard ground, the trowel may not cut through the soil quickly enough to prevent the spider from escaping. However, hard soil also increases the difficulty of digging, whether for pitfall trap placement, or for directly removing a spider from its burrow.

Tenebrio molitor are easy to obtain, simple to culture (Martin et al 1976), and larvae are resilient to field conditions, such as temperature fluctuation (pers. obs). However, *T. molitor* do require space, maintenance, and must be handled carefully to prevent damage. Recently pupated, teneral beetles are particularly fragile due to their soft cuticle, and therefore should not be tethered. Laboratory-raised *T. molitor* may also be prohibited from some protected offshore islands (e.g., Codfish Island), so other invertebrate bait would be required to capture idiopids (e.g. amphipods; Fig. 4.1B).

Unlike current popular methods for collecting trapdoor spiders, such as digging, beetling must be conducted at night, when the spiders are most active. Several populations can be located during the day, but collection of individuals is limited to two to three populations only. Spider responsiveness appeared to decline after a few hours of darkness.

The limitations of using tethered beetles to collect idiopid specimens are minor in comparison to the advantages. Beetling is a simple and easily executed method to lure both male and female idiopids from their burrows without disturbing the burrows or surrounding habitat.

4.4.5 Wider implications

In addition to luring *Cantuaria* from their burrows, beetling also attracted other species of fossorial predatory invertebrate. I did not investigate beetling as a possible method of capturing other invertebrates, but it could potentially be used to capture any fossorial predatory animal that relies on tactile information from the surface to detect prey.

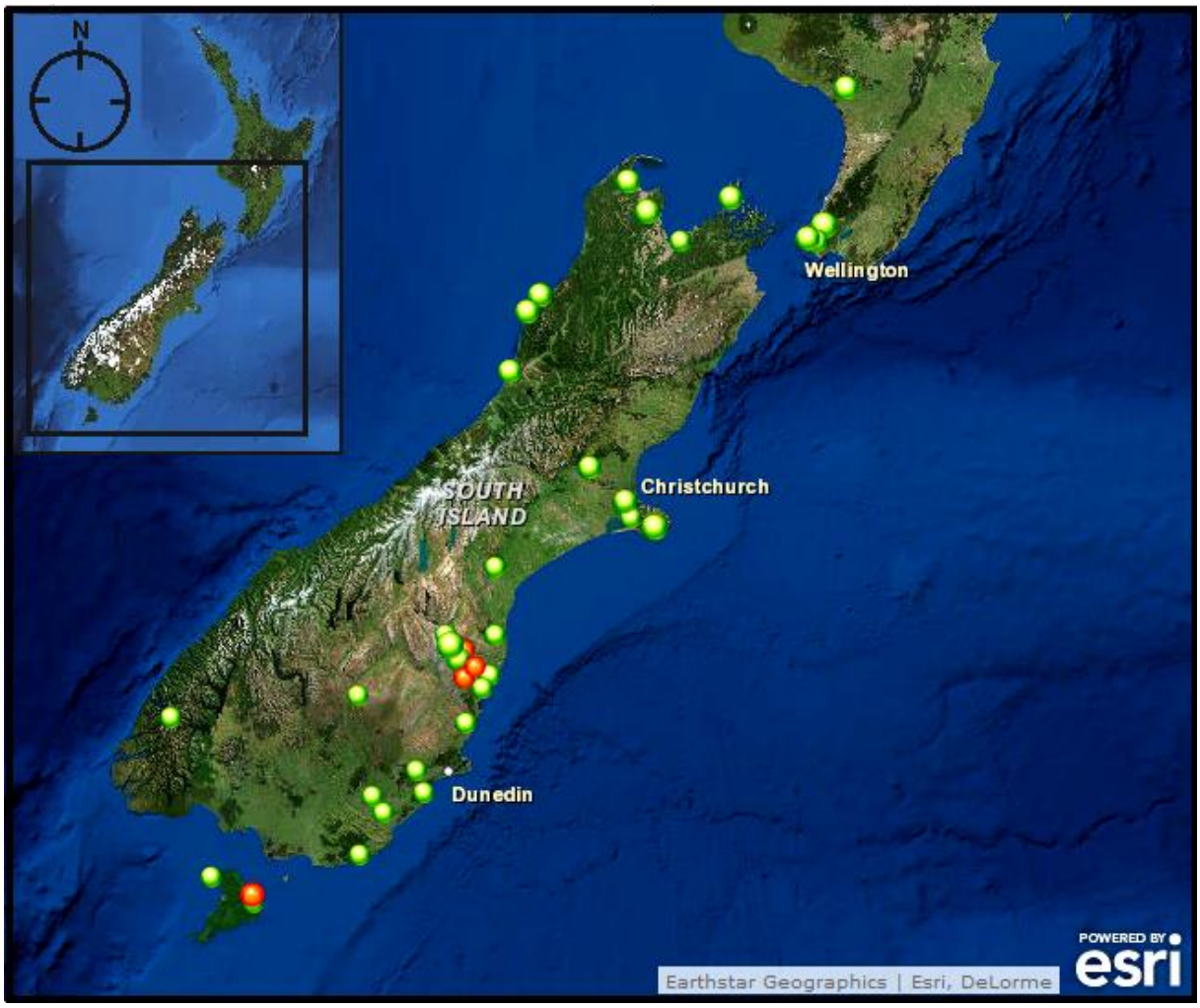

Figure 4.4: Map of collecting sites where beetling was successful (green markers) and unsuccessful (red markers).

Chapter 5
The phylogenetics and biogeography of Cantuaria

5.1 Introduction

The evolutionary history of a group of organisms can be visualised by constructing their phylogenetic relationships. Using modern algorithms, such as Bayesian or maximum likelihood to analyse differences between organisms, their patterns of divergence can be inferred. Bayesian and maximum likelihood inferences have been used to infer molecular phylogenies in many different taxa (e.g. cicadas; Arensburger, Simon & Holsinger 2004, galaxiid fish; Waters, López & Wallis 2000, birds; Jarvis et al. 2014, and lycosid spiders; Vink & Paterson 2003). Molecular techniques for species delimitation allow for the identification of cryptic species, which morphological data do not always reveal (Belfiore et al. 2003; Hamilton, Formanowicz & Bond 2011; Starrett & Hedin 2007). Evolutionary patterns are important to consider when evaluating a group's taxonomy, such as whether a given population is the same species as a nearby population, or whether the two may be different species (e.g. rodents; Belfiore, Hoffman, Baker & Dewoody 2003); theraphosid spiders (Hamilton, Formanowicz & Bond 2011); antrodiaetid spiders (Starrett & Hedin 2007). Molecular methods can be used to delimit species within a population without constructing a phylogeny. However, if there are many populations and different species within a genus, a phylogeny must be constructed to determine relationships within and between species across the whole genus. Discerning species statuses within a genus can inform conservation and management decisions; if a particular species is only represented by one threatened population, then that population must be conserved in order to preserve the species as a whole (e.g. Fountain et al. 2013). Additionally, phylogenetics is an integral part of studying the biogeography of a taxon, as inferences can be made based on where an organism's closest relatives are found. Particularly where speciation is allopatric, a molecular phylogeny can indicate when two groups of organisms became geographically separated, especially when a molecular clock is applied (Avise 2000).

Previous studies have shown that mygalomorphs in general, and trapdoor spiders in particular, have limited dispersal ability and a high degree of local endemism (Bond & Stockman 2008; Hedin et al. 2013; Satler et al. 2011; Starrett & Hedin 2007). In the past, mygalomorphs' lack of dispersal ability has been assumed to prevent them from crossing large expanses of ocean (Ferretti, Pérez-Miles & González 2010; Raven 1980), with the exception of those few genera that can balloon (e.g. *Atypus;* Pétillon et al. 2012; *Ummidia* and *Sphodros;* Coyle 1983; Coyle et al. 1985). The apparent lack of mygalomorphs on oceanic islands was attributed to their inability to disperse (Raven 1980), until the discovery on Hawa'ii of two species in the genus *Nihoa* (Barychelidae) (Churchill & Raven 1992; Raven 1988). There is also recent evidence that a

species in the African genus *Moggridgea* (Migidae) may have undergone oceanic dispersal to become the only known member of its genus present in Australia (Harrison et al. 2016).

The genus *Cantuaria* was last examined taxonomically by Forster and Wilton (1968), who described 42 different species based on morphology, primarily of the genitalia. The evolutionary relationships between members of the genus were hypothesised, but no phylogeny was constructed. Thirteen species represented a different ecotype from the others, with open or partially open burrows rather than fully lidded burrows, and morphological differences in the female genitalia (see Fig. 1.2). These species, known as the *huttoni* group, were included in the genus *Cantuaria*, but Forster and Wilton (1968) suggested that they may not be congeneric. There are many ecological, behavioural and morphological differences between the two ecotypes; for example, adult *C. johnsi* collected in Denniston and Greymouth were 30 mm long, but those collected on Stewart Island were only 5–10 mm long (pers. obvs.). Many characters used by Forster for distinguishing between species may not have been diagnostic; the male genitalia appear to be relied upon heavily for species diagnosis, but males have not been found for many species. Other characteristics, such as tarsal claws, appear to vary between females of the same species (pers. obs.). There are also likely to be many undescribed species (Raven, pers. comm).

Resolving *Cantuaria*'s evolutionary relationships is necessary to form a base on which to build biogeographic inferences. Phylogenies are an essential part of most modern biogeographical analyses (Morrone 2013). Phylogenetics has been incorporated into myriad biogeographic analyses of hundreds of animal taxa, including reptiles (Longrich et al. 2015), birds (Barker et al. 2015), and spiders (Starrett & Hedin 2007). *Cantuaria* species are the only described idiopid genus that can be found in New Zealand (though there is evidence for splitting *Cantuaria* into two separate genera; see Chapter 6). They have previously been considered endemic, indicating that the original divergence may have been allopatric. However, Rix (2015 pers. comm) noticed that *Euoplos annulipes* Koch, 1841, which is common in Tasmania, has morphology that closely resembles *Cantuaria*. Sequencing revealed *E. annulipes* to be sister to the rest of *Cantuaria*: it therefore appears to be a Tasmanian representative of *Cantuaria*, suggesting that *Misgolas* and *Cantuaria* diverged in Australia. The approximate date at which the *Cantuaria* lineage diverged from other idiopid lineages can be discerned using a dated phylogeny (Beck 2008; de Boer et al. 2015; Liu et al. 2016; Schaefer et al. 2009). Morphologically (Forster & Wilton 1968) and genetically (M. Rix, unpublished manuscript), *Cantuaria* is similar to the Australian genus *Misgolas*. The time at which the two lineages coalesced may have been within the last 25 million years, indicating that *Cantuaria* dispersed to New Zealand, and arrived at the end of the Oligocene drowning period (Trewick & Bland 2011; Waters & Craw 2006). Many of New Zealand's fauna appear to have dispersed across the Tasman Sea, including many bird species, skinks (Chapple et al. 2009), freshwater fish (Waters et al. 2000), and cicadas (Arensburger et al. 2004; Buckley et al. 2002) (see Wallis & Trewick

(2009) for a review). Alternatively, *Cantuaria* and *Misgolas* may have diverged before the Oligocene drowning, in which case *Cantuaria* may have been in Zealandia when it split from the rest of Gondwanaland. To determine which scenario is more likely, a dated phylogeny of the genus *Cantuaria*, with *Misgolas* as an outgroup, is constructed. The monophyly of *Cantuaria*, with *Misgolas* as its sister taxon, has been confirmed in an independent study (M. Rix, unpublished manuscript).

Understanding the relationship between *Cantuaria*'s evolutionary history and its distribution is vital to the study of *Cantuaria* biogeography. For example, are two different species found 100 km apart more closely related to each other than either species is to a third species that is 200 km away? Isolation by distance testing (IBD) is a method of determining how geographic distance affects genetic differentiation between populations (Wright et al. 2015; Wright 1943), and can be combined with phylogenies to examine relationships between distribution patterns and phylogenetics (Smith, Hallwachs & Janzen 2014; Trontelj & Utevsky 2012). Dating the phylogeny creates a picture of the evolutionary history of *Cantuaria* in space and time, allowing inferences to be made concerning how major events have affected the distribution and evolution of *Cantuaria* species.

Sequencing the DNA of *Cantuaria* species would enable investigation into whether currently accepted species (based on morphology) are supported by molecular evidence, and which species and populations are the most important to conserve if genetic diversity is to be preserved. In particular, cryptic species can be difficult to distinguish morphologically, and may only be reliably identified using molecular methods such as molecular phylogenetics (Belfiore et al. 2003).

New Zealand's shape, size, and topography have changed constantly since its formation (Trewick & Bland 2011; Wallis & Trewick 2009). Therefore, calibration dates for molecular clocks must be chosen carefully; a single feature, such as a mountain, river or strait, may have formed, disappeared, and been replaced by another similar feature over the last 25 my, cyclically isolating and connecting different habitats. Since no fossil Idiopidae have ever been identified, and a substitution rate has not yet been calculated for *Cantuaria* or any other idiopid, the genus' molecular clock cannot be precisely calibrated. As such, dates on internal nodes should be considered approximate.

If *Cantuaria* species diverged from their most recent common ancestor (MRCA) with *Misgolas* less than 25 mya, that would indicate that *Cantuaria* dispersed from Australia to an emergent New Zealand. On the other hand, if their MRCA is hypothesised to be between 80–35 mya, the ancestor of modern *Cantuaria* species would likely have begun their journey away from their closest relatives in Australia before New Zealand had emerged from the Oligocene drowning. However, if the MRCA node is estimated to be around 80 mya or older, that would suggest that the *Cantuaria* lineage may have diverged from the *Misgolas* lineage while they were both

coexisting on the supercontinent Gondwanaland (assuming the pattern is not caused by the extinction of lineages, which cannot be inferred from the data). This could have been due to *Cantuaria* diverging from *Misgolas*, but in Australia for millions of years before dispersing to New Zealand and dying out in Australia. Alternatively, and particularly if the divergence coincides with the split of Zealandia from the rest of Gondwana, the *Cantuaria* lineage diverged from the *Misgolas* lineage due to their physical separation as the *Cantuaria* lineage drifted on Zealandia away from the *Misgolas* lineage.

5.1.1 Research aim and objectives

The aim of this chapter is to investigate evolutionary relationships between *Cantuaria* populations and species. By constructing a dated phylogeny, I will be able to uncover how long *Cantuaria* have been separated from their sister genus *Misgolas*. Using phylogeographic techniques, I will be able to reconstruct how *Cantuaria* spread across New Zealand to reach their current distribution. *Cantuaria* is hypothesised to be a dispersal-limited genus, with a biogeographic history that reflects New Zealand's geological history. The divergence date between *Cantuaria* and *Misgolas* is thus hypothesised to be around 80 mya, and *Cantuaria* will show a clear pattern of divergence based on geological barriers, such as the Southern Alps mountain range. This chapter will address the following research questions:

1. What are the phylogenetic relationships between current populations and species of *Cantuaria*?
2. Approximately when did the *Cantuaria* lineage diverge from the *Misgolas* lineage?
3. What was the pattern of spread from the origin of *Cantuaria* in New Zealand to its current distribution?
4. What do phylogenetic and phylogeographic data reveal about the relative roles of dispersal and vicariance in *Cantuaria*'s history of distribution?

5.2 Methods

5.2.1 Sampling

Cantuaria species live in cryptic burrows in soil. The methods I used to capture samples are more comprehensively outlined in Chapter 3. Suitable habitat was searched in daylight, by eye, for burrows, which were marked and revisited after dark. A tethered beetle was used to lure each spider out of its burrow. Most of the specimens used in this study were caught using this method, but some (particularly males) were collected using pitfall traps, or found and handed in by members of the public. Areas were searched based on previous sightings of *Cantuaria*, and locations taken from Forster (1968). Additional locations were searched based on knowledge of

the types of habitat *Cantuaria* species appear to prefer; particularly clay banks at low or medium elevation, with minimal rock, and no tiger beetle burrows. Specimens (particularly males) were also sent in by members of the public. Three tissue samples from the genus *Misgolas* (*M. rapax*, *M. robertsi* and an unknown species) were donated by Michael Rix from the Western Australian Museum. *Misgolas* is sister genus to *Cantuaria*, according to current genetic and morphological evidence (M. Rix, unpublished manuscript). A full list of specimens used in this study, along with their collecting locations, is provided in Appendix F.

5.2.2 Laboratory sequencing

Genomic DNA was extracted from the femur muscles of specimens using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA) or ZR Genomic DNA™-Tissue MiniPrep (Zymo Research) kit, following the manufacturers' protocols. Lysis was carried out for 24 hours. Extracted genomic DNA was stored at -20°C until use.

Genes were chosen based on previous successful amplification in spiders, particularly mygalomorphs, and on rate of evolution. Three genes were amplified from the genomic DNA of each specimen: two nuclear genes (nDNA) (internal transcribed spacers (ITS 1 and 2; Bond & Stockman 2008) and histone three (H3; Opatova & Arnedo 2014; Opatova, Bond & Arnedo 2013), and one mitochondrial gene (mtDNA) (cytochrome oxidase 1 (CO1; Barrett & Hebert 2005; Starrett & Hedin 2007). The mitochondrial gene and internal transcribed spacers were selected for their fast substitution rates to resolve shallower nodes, with H3 being a slower-evolving gene, so that deep nodes could also be resolved with confidence. Preliminary phylogenies were constructed in BEAST V2.3.1. Individuals representing different major clades in the preliminary phylogeny (separated by genetic distances of at least 15%) were selected for a four-gene time-calibrated phylogeny. The individuals were chosen after preliminary genetic analysis to discover which combination of individuals would best represent the genus, taking into account how many genes had been successfully sequenced for those individuals. For those selected individuals, the mtDNA gene cytochrome b (cytb) was also amplified. Genes were selected based on their provision of a range of substitution rates, and ease of amplification. Each gene was amplified using polymerase chain reaction (PCR). Several taq polymerases were tested; the most successful taqs were iTaq (BIO-RAD Laboratories, Hercules, CA, USA) and MyTaq (Bioline, Cambridge, UK). Mastermix ingredients and PCR parameters used are outlined in Table 5.1.

Table 5.1: Polymerase chain reaction master mixes and parameters for each gene after optimisation

Gene	Primers	Mastermix (for 10 ul reaction)		PCR parameters			
Cytochrome C oxidase subunit 1 (CO1): mtDNA	C1J1517 (5'-AATCATARGGATATTGGAAC-3') C1N2776-spider (5'-GGATAATCAGAATANCGNCGAGG-3')	Ingredient	Volume (ul)		1 cycle	35 cycles	1 cycle
		Primers (20 um solution, forward and reverse)	0.39	Temp (°C)	94	94-49-72	72-4
		10X iTaq Buffer	0.99	Time (mins:secs)	2.00	0.20-0.45-1.30	5.00-∞
		10 mM dNTPs	0.99				
		5X Betaine	0.1				
		Water	6.22				
		iTaq	0.1				
		BSA	0.5				
		DNA template	0.32				
Internal transcribed spacers (ITS): nDNA	CAS18SF1 (5'-TACACACCGCCCGTCGCTACTA-3') CAS28SB1d (5'-TTCTTTTCCTCCSCTTAYTRATATGCTTAA-3')	Primers (20 um solution, forward and reverse)	0.39	Temp (°C)	94	94-55-72	72-4
		Buffer	0.99	Time (mins:secs)	2.00	0.20-0.40-1.30	5.00-∞
		dNTPs	0.99				
		Water	6.34				
		iTaq	0.08				
		BSA	0.5				
		DNA template	0.32				
Histone 3 (H3): nDNA	H3F (5'-ATGGCTCGTACCAAGCAGACVGC-3') H3R (5'-ATATCCTTRGGCATRATRGTGAC-3')	Primers (20 um solution, forward and reverse)	0.32	Temp (°C)	94	94-60-72	72-4
		Buffer	1.0	Time (mins:secs)	2.00	0.20-0.10-0.50	10.00-∞
		dNTPs	1.0				
		MgCl2	0.08				
		Betaine	0.04				
		Water	6.36				
		iTaq	0.1				
		BSA	0.5				
		DNA template	0.28				
Cytochrome b (CytB): mtDNA, subsampled individuals only	CYBJ10612_Id_f1 (5'-CCKTCTAGAATYTCKTATWTGTGRA-3') CYB_Id_r1 (5' -AAARTATCACTCRGGCTGRAT-3')	Primers (20 um solution, forward and reverse)	0.2	Temp (°C)	95	95-48-72	4
		MyTaq Reaction Buffer	2.0	Time (mins:secs)	1.00	15-15-10	∞
		Water	7.1				
		MyTaq	0.1				
		DNA template	0.4				

Every PCR reaction had a negative control. Polymerase chain reaction products were checked for amplified genes using gel electrophoresis. A 1.5% agarose gel stained with SYBR Safe TM DNA Gel Stain (Molecular Probes, Eugene, Oregon) was used to run the samples, and results were viewed under ultraviolet light. PCR products were sequenced bi-directionally using 0.8 µM of primer, BigDye version 3.1 (Applied Biosystems, Warrington, Cheshire, UK) and the following thermal regime: 96°C for 1 min followed by 25 cycles of 96 °C for 10 s, 50 °C for 5 s and 60°C for 4 minutes. Samples were sequenced in an AVANT 3100 (ABI) capillary sequencer.

5.2.3 Phylogenetic analysis

Sequence chromatograms were viewed using FinchTV (Geospiza, Inc 2015). Any ambiguous nucleotides were replaced with N. An alignment was created for each gene in MEGA 5 (Koichiro Tamura et al. 2011); the sequences were aligned using the software, PRANK (Löytynoja & Goldman 2010). Phylogeny-aware alignment algorithms, such as PRANK, have consistently out-performed popular progressive alignment tools, such as CLUSTAL (Larkin et al. 2007) and MUSCLE (Edgar 2004) (Loytynoja & Goldman 2008). The ends were trimmed until the first and last bases in each alignment had at least 60% sequence coverage. Trimmed alignments of protein-coding genes (CO1, CytB and H3) were then put into the correct reading frame by deleting the first one or two base pairs in the alignment. Some H3 sequences had low quality data at positions 241, 246, 247 and 248.

Molecular substitution models were tested using JModeltest (Darriba, Doallo, Posada & Taboada 2012) using only five substitution schemes to limit the complexity of the models tested. Akaike information criterion, corrected for small sample size (AICc; Hurvich & Tsai 1993), was used to select the model that best fit the data (Table 5.1). Best topology (which calculates both nearest-neighbour interchange (NNI) and subtree pruning and regrafting (SPR) topologies, then selects the result that best fits the data) was used. Protein-coding gene alignments were tested using PartitionFinder (Lanfear et al. 2012) to find the optimal partitioning scheme. Models selected are shown in Table 5.2.

For single locus phylogenies, BEAST (Drummond et al. 2012) .xml files were compiled using Bayesian Evolutionary Analysis Utility (BEAUti; Drummond et al. 2012). Initially, each alignment was imported into BEAUti as a NEXUS file, with partitions defined as character sets. *Misgolas* sequences were monophyletically constrained to act as outgroups, and models selected according to those suggested by JModeltest (Table 5.2). Analyses were run under relaxed lognormal molecular clocks using the coalescent constant size prior. Each preliminary run consisted of one million generations with sampling every 1000 steps. The results of each run were examined using Tracer (Rambaut & Drummond 2007) to check the parameter estimates and convergence. If the mean of the standard deviation parameter (ucld. stdev) estimate was >1, a random clock was tested; otherwise, both strict and random local clocks were tested to see their effects on effective sample size (ESS) values, and on convergence. When all priors and

parameters had been optimised, a run of ten million generations was implemented. Trees were then assembled in TreeAnnotator (Rambaut & Drummond 2013) and viewed in FigTree (Andrew Rambaut 2015).

Table 5.2: Substitution models (including site heterogeneity (gamma/inverse/inverse and gamma)) estimated by JModeltest and implemented in BEAST analyses.

Gene	Model
CO1	Tamura-Nei (inverse and gamma sites) (TrN+I+G; Tamura & Nei 1993)
H3	Kimura 1980 (inverse sites) (K80+I; Kimura 1980)
ITS	Symmetrical model (inverse and gamma sites) (SYM+I+G; Zharkikh 1994)
CytB	Hasegawa-Kishino-Yano (inverse and gamma sites) (HKY+I+G; Hasegawa, Yano & Kishino 1984)

When BEAST runs had been optimised for each locus individually, the same alignments and settings were input into a *BEAST multilocus analysis (Heled & Drummond 2010). For the deeper divergence phylogeny, CytB sequences were used alongside CO1, ITS, and H3 sequences to construct a phylogeny consisting of representatives of the major *Cantuaria* clades (i.e. differing in mitochondrial sequences by at least 15%), plus two outgroup *Misgolas* sequences. This "deep phylogeny" was less computationally intensive, and had higher posterior probabilities, than attempts at building a complete multilocus phylogeny, and each terminal node was represented by at least two different gene sequences.

A third phylogeny was constructed, using *BEAST, which contained only individuals for which sequences from at least two genes had been obtained. Only the H3, CO1, and ITS alignments were used. After examining the resulting phylogeny, individuals with low (<0.4) posterior probabilities at the MRCA were removed from the dataset and the analysis run again without them. The resulting tree had fewer low posterior probability branches (all posterior probabilities > 0.4, 7 posterior probabilities <0.8). Clades with low credibility (<0.8 posterior probability) were collapsed using Mesquite (Maddison & Maddison 2016) to form polytomies. The resulting tree was a representative of *Cantuaria* sequences collected throughout New Zealand, and included all the major clades of the complete tree, but was simplified to include only nodes with posterior probabilities >0.8. This "geophylogeny" was constructed to be input into geographic analyses in GenGIS (Parks et al. 2009). The sequences included in the geophylogeny were used in IBD analyses in Alleles in Space (Miller 2005).

Since no idiopid fossils have yet been found, and no precise substitution rates have been estimated for the *Cantuaria* genus, calibration of molecular clocks was carried out using both substitution rates (calculated from a closely related spider family) and geological dates. A recently estimated ctenizid mitochondrial substitution rate (0.0444 substitutions/site/million years) (Kornilios et al. 2016) was specified as the clock model rate for the CO1 dataset. The rates for the other genes were instructed to be estimated based on the CO1 rate. A different tree was constructed using the substitution rate calculated for arthropods (0.0269

substitutions/site/million years) (Papadopoulou, Anastasiou & Vogler 2010), which has been shown to be close to the rate for araneomorphs (Bidegaray-Batista & Arnedo 2011).

In addition to the trees dated using substitution rates, three sets of two trees were created identical to the geotree and deep divergence tree. These trees were calibrated using geological dates: the MRCA of *Misgolas* and *Cantuaria* was set as a prior (M. Rix, unpublished manuscript), with initial estimates between 22 and 80 million years (coinciding with the growing rift between Zealandia and the rest of Gondwanaland; Gibbs 2006; Mortimer 2004; Waters & Craw 2006). Additionally, the MRCA of the West Coast *Cantuaria* specimens was dated at 5-10mya to coincide with the rise of the Southern Alps (Fleming 1979; Mildenhall et al. 2014; Mortimer 2004; Trewick & Bland 2011). One set of trees was dated using both of these geological dates; another set was dated using only the 22-80 mya Gondwanan split; the third set of trees was dates using only the rise of the Southern Alps.

5.2.4 Data analysis

Both the deep divergence tree and the geophylogeny, were input into the program GenGIS v. 2.5.0 (Parks et al. 2009) along with the GPS coordinates where each individual represented in the tree was collected. Terminal nodes were linked to their locations and superimposed upon a map. A Monte Carlo permutation test was then carried out in GenGIS. Each permutation randomly and temporarily changes the ordering of geographic points along the "geographic layout line" (a line which associates terminal nodes to their locations, which is redundant in my analysis as each node is from a different location, so is not shown), finds the optimal ordering of leaf nodes (to minimise the number of "crossings", or times the lines cross between terminal nodes and their geographic locations), and then counts the number of crossings. An automatically generated graph plots the numbers of crossings obtained in the permutations against the total number of times they occurred during the test. The fraction of permutations that have a number of crossings fewer than, or equal to, the number of crossings in the original model is reported as a p-value; the lower the p-value, the lower the chance that the number of crossings in the original model could be obtained by chance alone. The p-value can be used as a frequentist test of significance, but due to the various flaws in relying on p-values alone to reject hypotheses (e.g. Halsey et al. 2015), the graph was interpreted holistically, using the p-value as the point at which my data lie compared to the randomly-generated image of what the data would show if *Cantuaria* species were randomly distributed across New Zealand.

Subsampled CO1 and H3 alignments were uploaded alongside their associated geographic coordinates into Alleles in Space (AIS) (Miller 2005). Due to the limitations of AIS, the sequences had to be shortened so as not to include gaps, and shorter sequences had to be removed; the ITS alignment was excluded from analysis due to its high number of gaps distributed throughout the alignment. A Mantel test for IBD was then conducted.

5.3 Results

Between 2013–2015, a total of 226 specimens were collected from 76 locations throughout New Zealand (Fig. 5.1). After extracting all genomic DNA extractions from all specimens collected plus three outgroup extractions, 111 were successful in yielding at least one gene sequence. Although most specimens were represented by sequence data from only one gene, 39% of specimens yielded sequences from at least two genes. Difficulty in amplifying and sequencing was partially attributed to inhibitors present in the DNA, despite care in isolating femur muscle from cuticle. Running PCRs on a mixture of DNA from a sample that didn't amplify previously (negative) and DNA from a sample that did amplify previously (positive) resulted in no DNA amplification. Control tubes containing the same master mix and the positive DNA showed DNA amplification. The negative sample was therefore suspected to include inhibitors, preventing amplification of the DNA in the sample. Inhibitor removal kits (Zymo Research) aided in amplifying some samples. All ITS and CO1 sequences obtained were uploaded onto GenBank (Benson et al. 2010), and H3 sequences were uploaded onto FigShare (see Appendix F). Voucher specimens are held at Canterbury Museum, Otago Museum, the Lincoln University

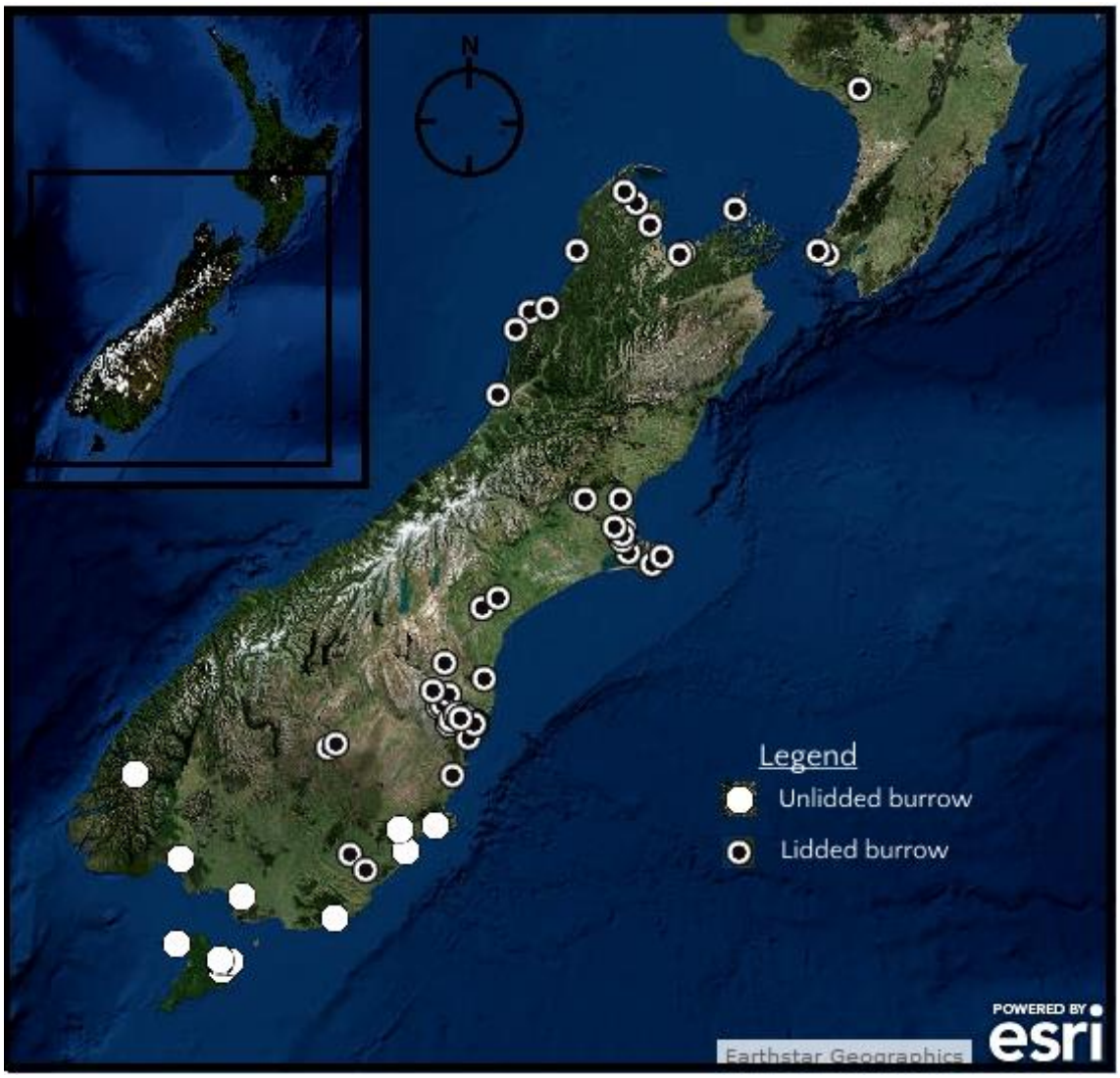

Figure 5.1: Map of locations where *Cantuaria* were collected for sequencing. Filled circles represent specimens collected from populations with lidded burrows; unfilled circles represent specimens collected from populations with unlidded burrows.

Entomology Museum, the Museum of New Zealand, and the Natural History Museum in London (Appendix D).

5.3.1 Phylogenies

A strict clock model was found to be optimal for all phylogenies. The mean standard deviation was less than 1 in all runs, and runs only converged and showed ESS values >/= 200 under a strict clock.

Figure 5.2 shows the phylogeny created by the optimised BEAST run for CO1, which contained 59 taxa with 268–1133 bp (mean = 946). Although Partitionfinder suggested a partitioning scheme, its implementation overparameterised the model, so the partitioning scheme was not ultimately used.

According to the maximum clade credibility tree (Fig. 5.2), a clade containing two North Island specimens collected in Whanganui (and therefore assumed to be *C. wanganuiensis* (Todd, 1945); Forster & Wilton 1968) is sister to the D'Urville Island specimen. The D'Urville and Whanganui specimens form a clade that is the sister taxon to the rest of the genus *Cantuaria* (Fig. 5.2). Interestingly, specimens collected in Johnsonville and Days Bay, both in the North Island, are nested in a clade with specimens collected from Blenheim; however, the low posterior probabilities at mid-level between the root and the crown of the tree make some inferences unreliable. Figure 5.3 shows the phylogeny created by the optimised BEAST run for ITS, which contained 46 taxa with 346–987 bp (mean=770).

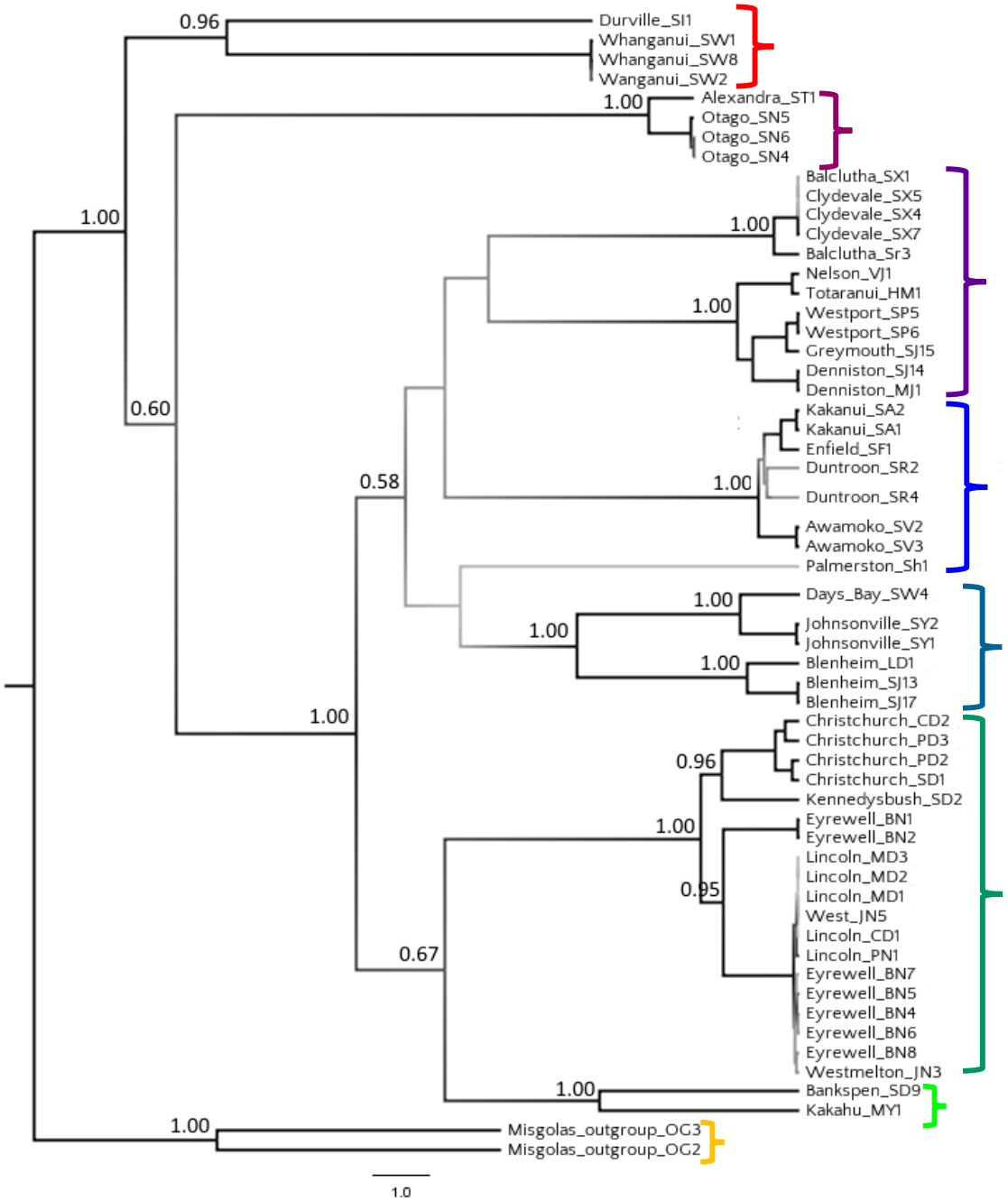

Figure 5.2: Maximum clade credibility tree for CO1. Taxa are labelled in the format location_specimen ID. Most specimens are female and cannot be identified based on morphology. Nodes are colour coded according to posterior probability, from low (light grey) to high (black). Posterior probabilities >0.50 are labelled at internal nodes. Brackets denote major clades for ease of tree comparison: from top to bottom, *wanganuiensis* clade, *toddi* clade, *johnsi* clade, *marplesi* clade, *myersi* clade, *dendyi* clade, *kakahuensis* clade, outgroups.

The ITS maximum clade credibility tree (Fig. 5.3) also shows that the specimen caught on D'Urville Island is the sister taxon to the rest of the genus, and in fact the branch between that sequence and the outgroup clade is shorter than the branch between the D'Urville specimen and the rest of *Cantuaria*. Interestingly, the specimens obtained from unlidded burrows form two clades: the *huttoni* and *orepukiensis* clade, and the *stewarti* clade. The *huttoni* and *orepukiensis* clade, which contain specimens obtained in Southland from unlidded burrows, is more closely related in the ITS tree than to the *stewarti* clade, which contains taxa found in Fiordland (including Stewart Island).

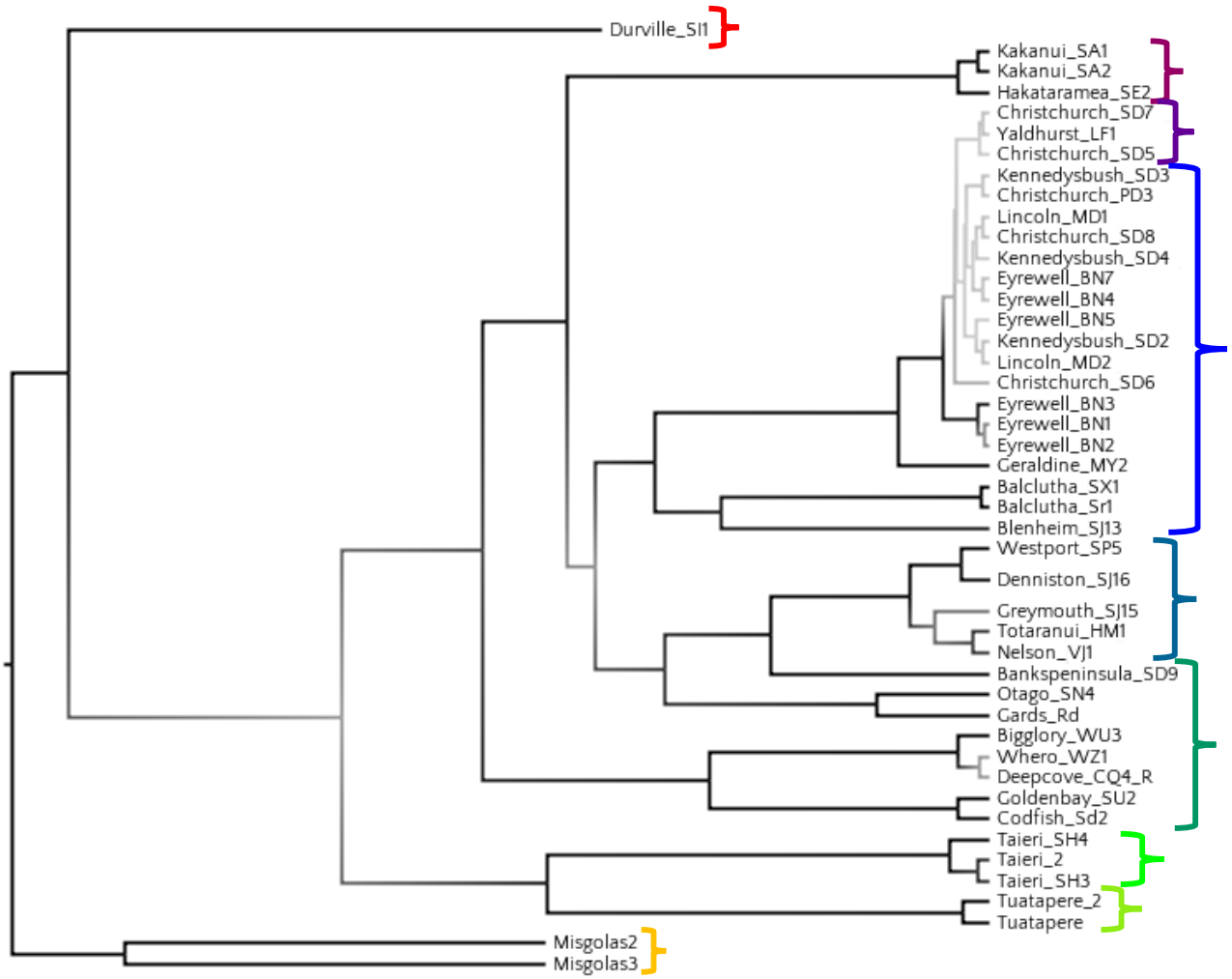

Figure 5.3: Maximum clade credibility tree for ITS. Taxa are labelled in the format location _specimen ID. Most specimens are female and cannot be identified based on morphology. Nodes are colour coded according to posterior probability, from low (light grey) to high (black). Posterior probabilities >0.50 are labelled at internal nodes. Brackets denote major clades for ease of tree comparison: from top to bottom, *insulana* clade, *stewarti* clade, *kakanuiensis* clade, *dendyi* clade, *depressa* clade, *johnsi* clade, *huttoni* clade (unlidded ecotype), *orepukiensis* clade (unlidded ecotype), outgroups.

Figure 5.4 shows the phylogeny created by the optimised BEAST run for H3, which contained 65 taxa with 196–320 bp (mean = 300). Since the H3 gene could not be amplified from any of the *Misgolas* extractions, the tree was rooted at the MRCA of the *huttoni* unlidded species and the rest of the genus. Monophyly of the *huttoni* group, and their position as the sister taxon to the rest of the genus, was supported by a phylogeny constructed with an outgroup *Segregara* sp. sequence from Genbank (accession number KM110596).

The H3 maximum clade credibility tree (Fig. 5.4) shows similar clade structure to the ITS and CO1 trees. In particular, the *johnsi*, *marplesi*, and *dendyi* clades appear to be relatively stable in all three phylogenies. The unlidded *huttoni* species are also monophyletic, showing a similar pattern to the ITS phylogeny in that the Fiordland specimens are in a separate clade, though the Southland specimens are paraphyletic. There is discrepancy between the three phylogenies. As most specimens are only represented by one sequence, and the posterior probabilities in all three phylogenies are highly variable, the results at a fine scale must be interpreted with caution.

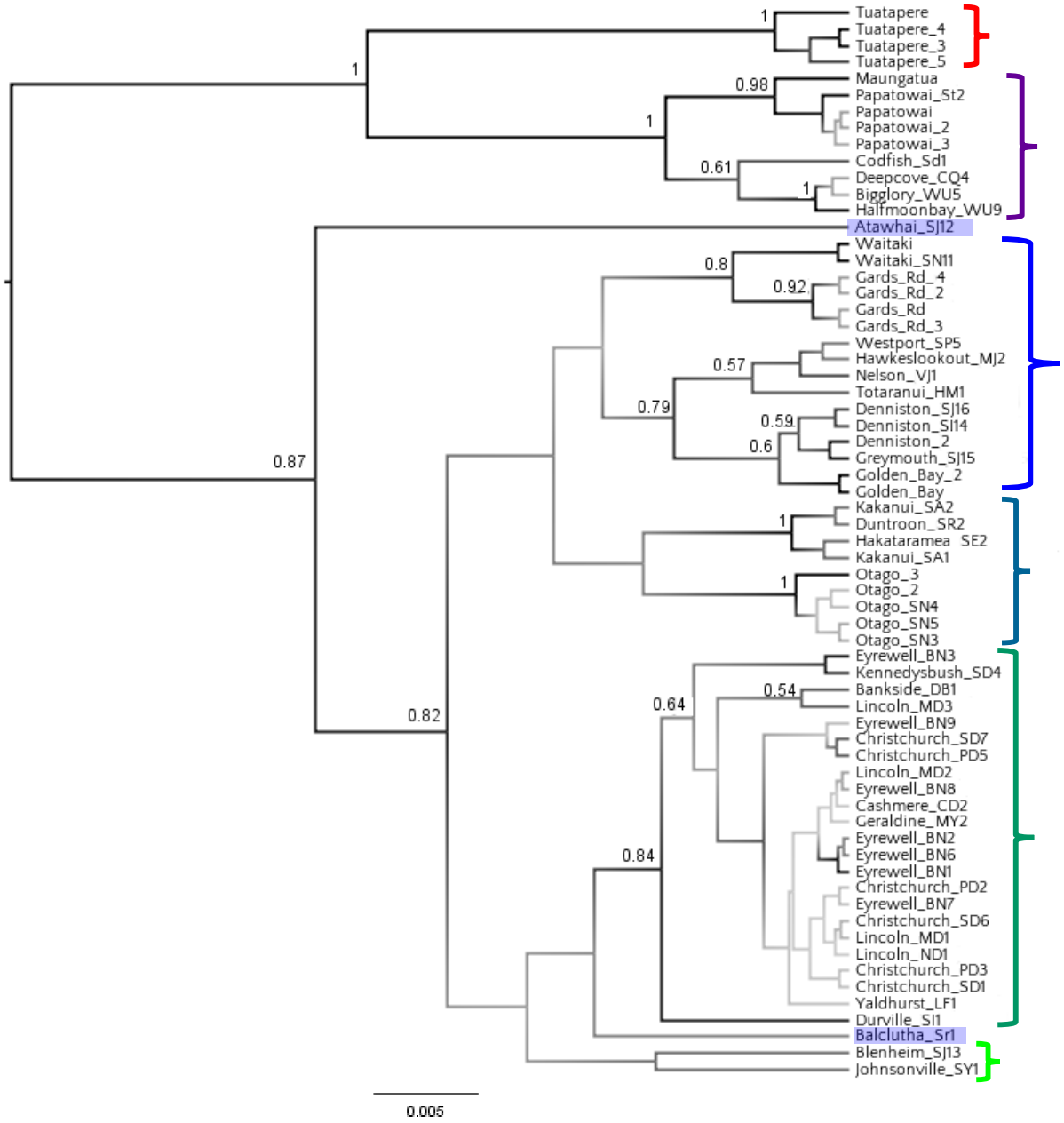

Figure 5.4: Maximum clade credibility tree for H3. Taxa are labelled in the format location_specimen ID. Most specimens are female and cannot be identified based on morphology. Nodes are colour coded according to posterior probability, from low (light grey) to high (black). Posterior probabilities >0.50 are labelled at internal nodes. Brackets denote major clades for ease of tree comparison: from top to bottom, *orepukiensis* clade (unlidded ecotype), *stewarti* clade (unlidded ecotype), *johnsi* clade, *marplesi* clade, *dendyi* clade, *myersi* clade. Two sequences with long branches that did not fit into clades are highlighted in purple.

The deep divergence phylogeny (Fig. 5.5) contained seven *Cantuaria* taxa and two outgroups. Running the deeper divergence tree using the arthropod substitution rate of 0.0269% (Papadopoulou et al. 2010) recovered a divergence date of 15.18 mya for the MRCA of *Misgolas* and *Cantuaria*. With the mygalomorph substitution rate (0.0444% as the clock calibration; Kornilios et al. 2016), however, a divergence date of 18.7 mya was estimated.

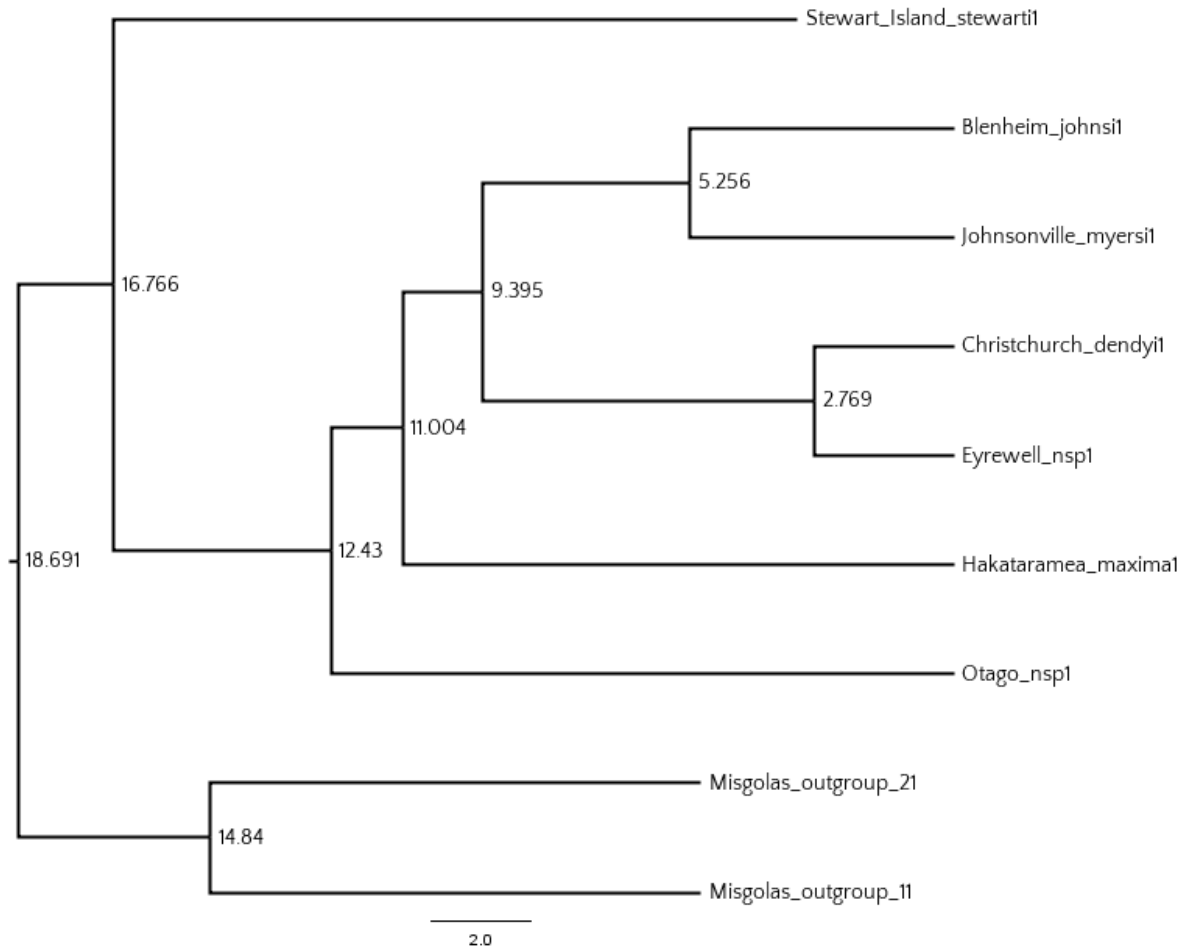

Figure 5.5: Maximum clade credibility tree for the deep divergence dataset. Taxa are labelled in the format location_species. Numbers distinguish similarly named taxa. Most specimens are female and cannot be identified based on morphology, so species is based mostly on collecting location and general morphology. Posterior probabilities are >0.99 at all nodes. The age of each node in millions of years is indicated by node labels.

The subset of sequences that best represents the geographical distribution of the genus *Cantuaria* without bringing the clade credibility below 0.45 contains 20 taxa and two outgroups (Fig. 5.6). Each taxon is comprised of individuals found in the same population, identified down to species as often as possible based on male genitalia, female general morphology (e.g. size and shape), and collecting location. Due to discrepancies between the different CO1, ITS and H3 gene trees, some clades have low posterior probability. *Cantuaria sylvatica*, representing the *huttoni*/*stewarti* clade, is the sister taxon to the rest of the genus in the geotree, with *C. insulana* also forming its own clade as the sister taxon to the other non-*huttoni* taxa, as in the ITS tree (Fig. 5.3). The *marplesi*, *dendyi* and *johnsi* clades are well-supported in the geotree. Using the mygalomorph mitochondrial substitution rate of 0.0444% (Kornilios et al. 2016), the divergence date between *Misgolas* and *Cantuaria* was estimated as approximately 16.72 mya.

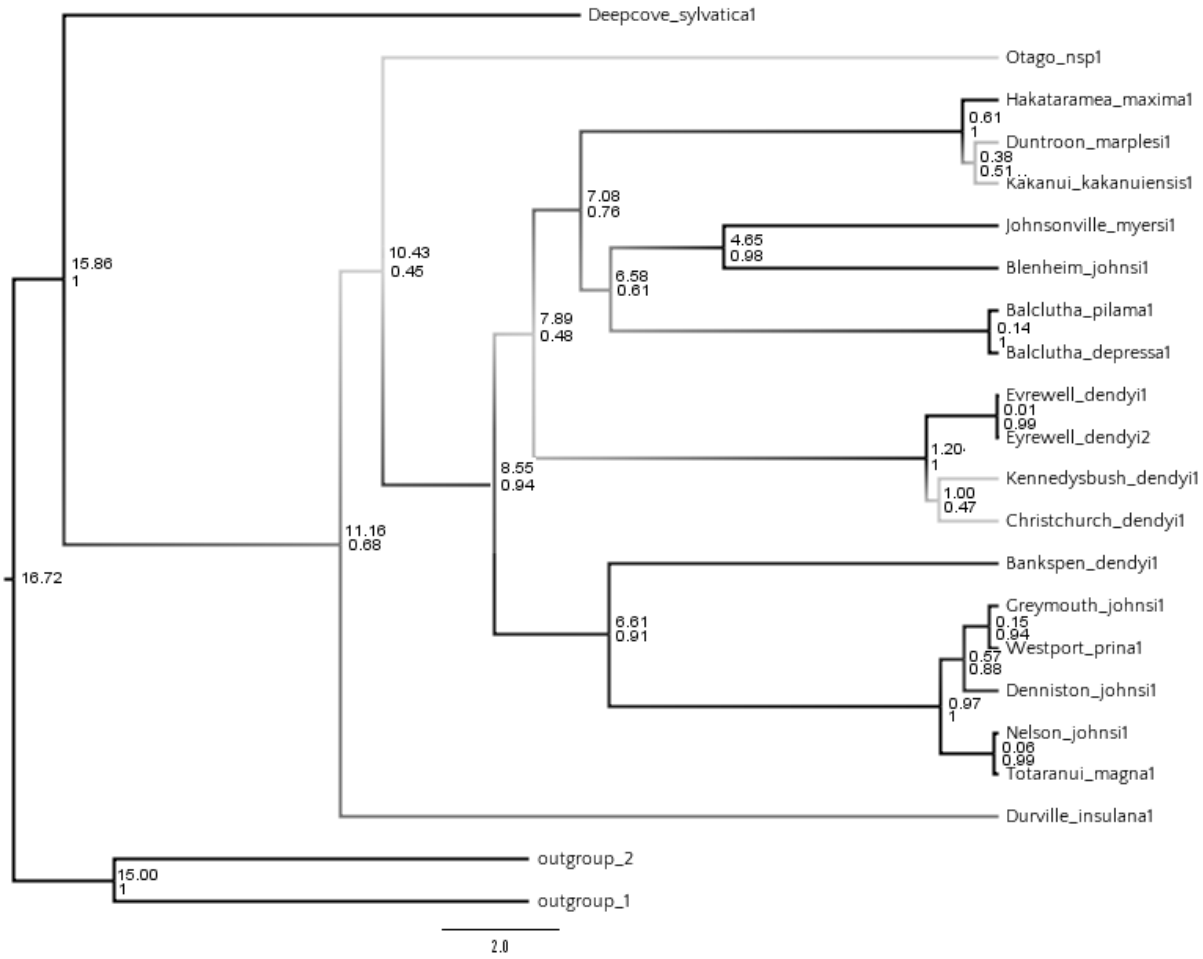

Figure 5.6: Maximum clade credibility *BEAST geotree. Taxa are labelled in the format location_species, with the numbers separating similarly named taxa. Most specimens are female and cannot be reliably identified based entirely on morphology, so species is based mostly on collecting location and general morphology. Nodes are colour coded according to posterior probability, from low (light grey) to high (black). Posterior probabilities and node ages are labelled at internal nodes; the top numbers indicate node ages (in millions of years), while the bottom numbers indicate posterior probabilities. Note that clades supported by a posterior probability of <0.8 were collapsed for the GenGIS analysis.

When the geotree was dated using both the rise of the Southern Alps (5–10 mya) and the split of Zealandia from the rest of Gondwanaland (22–80 mya), the tree failed to converge or reach an ESS of 200 for all parameters, even after 300 million generations. A tree calibrated using the split between Zealandia and the rest of Gondwanaland (using a uniform distribution with an upper limit of 80 and a lower limit of 22 as the time to most recent common ancestor (TMRCA)) recovered the date of divergence between *Misgolas* and *Cantuaria* as 125.7 mya. Eyrewell_1 and Christchurch_1, crown nodes that were separated by 2.8 my when dated using the mygalomorph substitution rate (Fig. 5.5), are separated by 20.7 my in the geologically dated phylogeny, indicating an extremely slow nucleotide substitution rate under this scenario. However, the geologically dated trees were slow to reach convergence, and ESS was below 200 in almost all parameters even after running the analysis for 300 million generations.

5.3.2 Biogeography

The deep divergence phylogeny, when loaded into GenGIS, showed a clear correlation between phylogenetic position and geographical location, with the most recently diverging clades positioned further north and the more deeply divergent lineages further south (Fig. 5.7). Samples in the *dendyi* clade (collected from Christchurch and Eyrewell) form a sister clade with similar branch lengths to specimens collected in Blenheim and Wellington. None of the lines connecting terminal node to specimen location crossed over (crossovers indicate genetic distances that do not correlate with geographic distances; many crossovers indicate more random distribution of populations). The permutation test found that the number of crossings observed was less than the number of crossings expected if terminal nodes were connected to random locations ($p=0.02$; Fig. 5.8). However, the more comprehensive geophylogeny did have some crossovers (Fig. 5.9), possibly partly due to increased stochasticity associated with the larger variability of posterior probabilities in the phylogeny (Fig. 5.6). However, the permutation test still found the number of crossings to be significantly lower than the number of crossings expected under a random model ($p<0.01$) (Fig. 5.10).

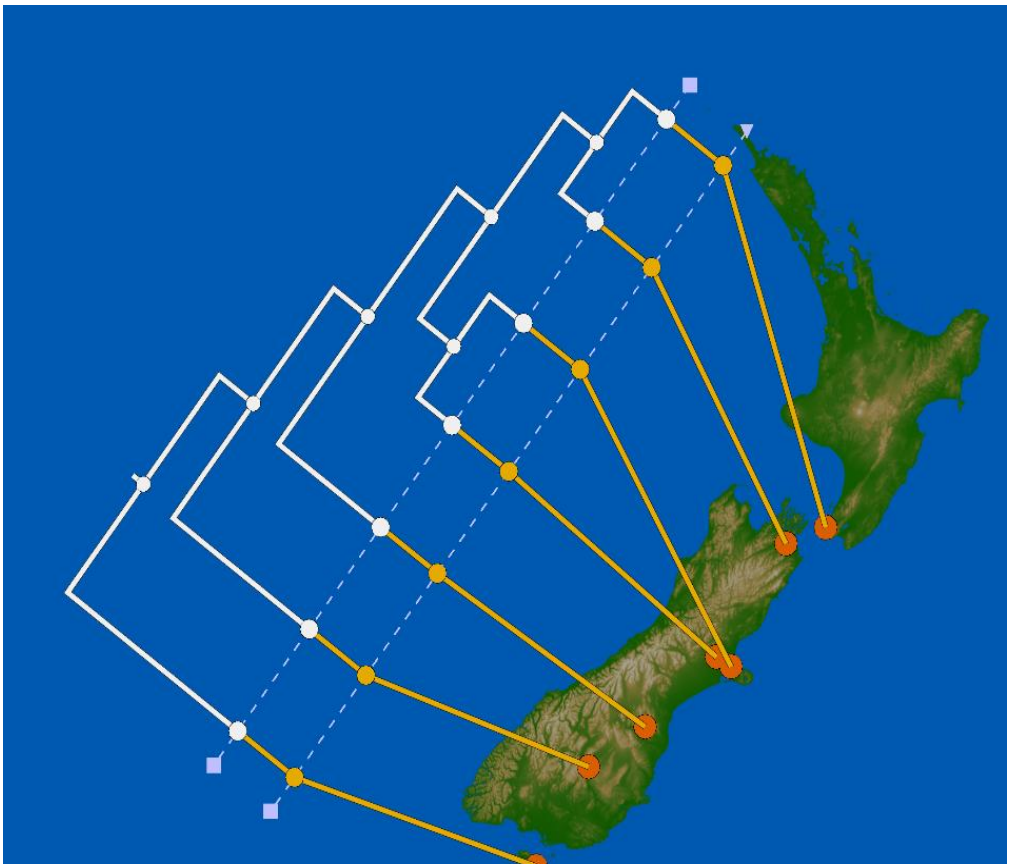

Figure 5.7: Mapped deep divergence phylogeny created in GenGIS. Orange lines connect terminal nodes of the phylogeny with their collecting locations on the map.

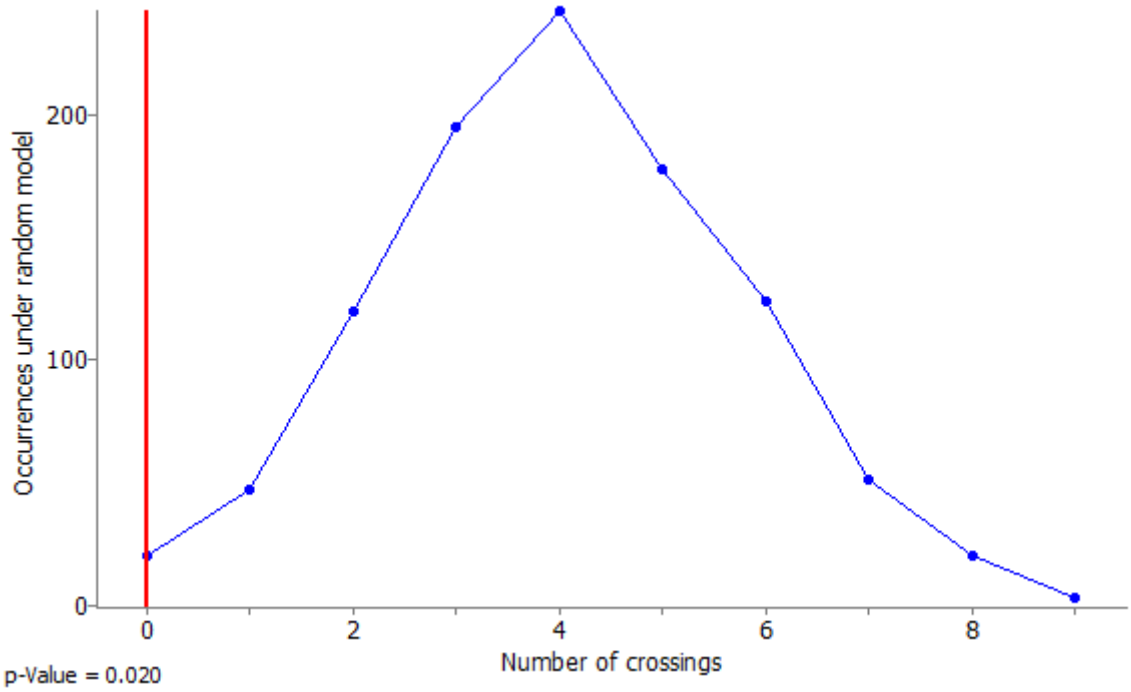

Figure 5.8: Results of the permutation test conducted on the deep divergence in GenGIS. The red line indicated the number of crossings observed in the data (0), while the blue line indicates the number of times each number of crossings is obtained under a random model (maximum number of crossings=8; most common number of crossings under a random model=4).

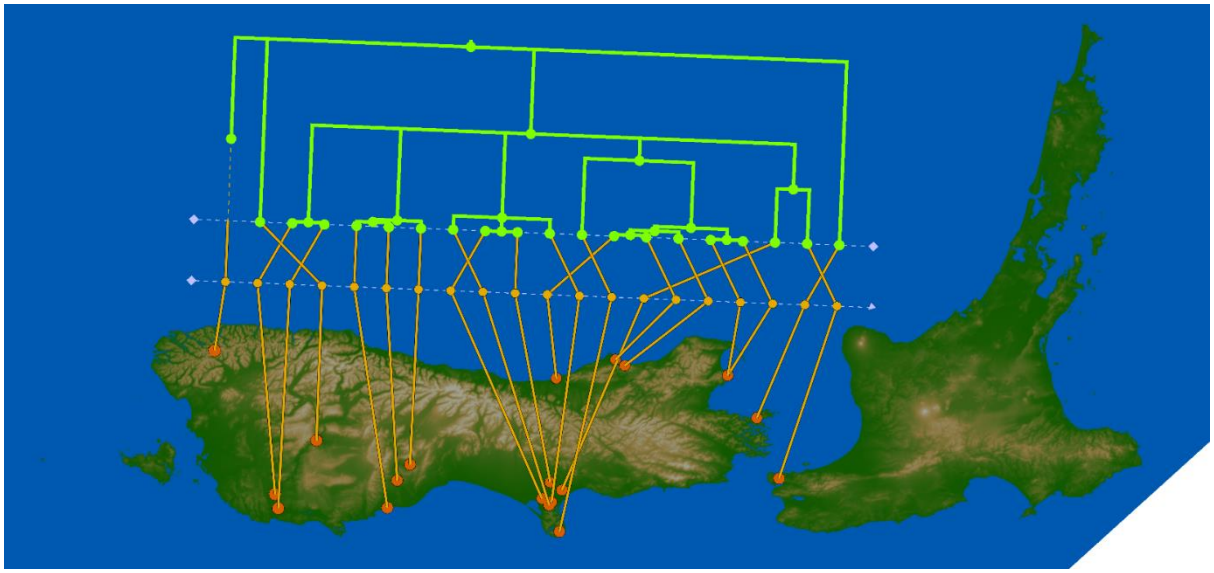

Figure 5.9: Mapped geophylogeny created in GenGIS. Orange lines connect terminal nodes of the phylogeny with their collecting locations on the map.

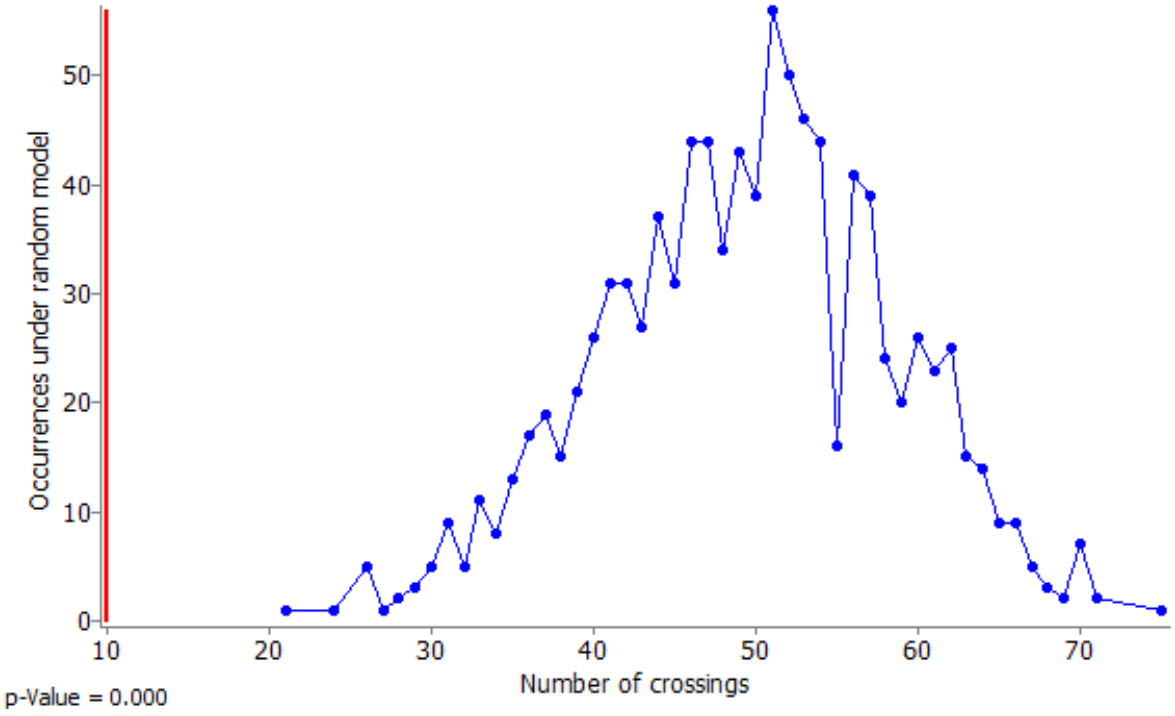

Figure 5.10: Results of the permutation test conducted in GenGIS. The red line indicates the number of crossings observed in the data (10), while the blue line indicates the number of times each number of crossings is obtained under a random model.

The Mantel test found evidence of IBD in CO1 (probability of observing a correlation between genetic and geographic distances greater than or equal to that observed (p) =0.001; correlation coefficient (r) =0.546). However, in the H3 dataset there was no evidence of IBD (p=0.42, r=.01).The CO1 dataset used in the Mantel test contained 17 sequences with 997 bp each; the H3 dataset contained 20 sequences of 196 bp each.

5.4 Discussion

My research provides evidence that a dispersal-limited idiopid genus may have nonetheless dispersed across the Tasman from Australia to New Zealand. My findings are the first example of an idiopid genus that has undergone oceanic dispersal. I combined molecular evidence with phylogeography to reveal evidence that a large number of species and a lack of dispersal ability do not necessarily exclude a history of long-distance dispersal.

The genus *Cantuaria* appears to have diverged from *Misgolas* approximately 18 million years ago, before dispersing to New Zealand across the Tasman Sea. The ages of the nodes recovered using different calibration methods (geological dating and substitution rate dating) were considerably different (15–18 million years *Misgolas*/*Cantuaria* divergence when dated using substitution rates; 125 million years when using geological dates). The large difference indicates that either the *Cantuaria* mitochondrial substitution rate is similar to that of its close relatives, and it dispersed to New Zealand after the waters subsided ca. 22–27 mya, or the mitochondrial substitution rate of *Cantuaria* differs massively from the substitution rates of both arthropods and mygalomorphs, and it diverged from *Misgolas* ca. 125 million years ago. The latter vicariance-based scenario would suggest that *Cantuaria* diverged from *Misgolas* before Zealandia began to split from the rest of Gondwana, indicating that the *Cantuaria* lineage would have survived on Zealandia and gone extinct in Australia. While possible, this scenario is less likely than the dispersal scenario, which suggests *Cantuaria* landed in the newly-emerged New Zealand at a similar time to other biota (Perrie et al. 2003; Waters et al. 2000), and does not require *Cantuaria*'s substitution rate to be much slower than that of other mygalomorphs. While mitochondrial substitution rates can vary greatly (e.g. 0.0444% for mygalomorphs, 0.0269% for araneomorphs and Opiliones; Kornilios et al. 2016; Papadopoulou et al. 2010), a vicariance scenario would require an unrealistic amount of variation in substitution rate speed to change the date of divergence from 18 mya to 125 mya. Even given the imprecision of molecular clock calibrations, and the low ESS of the geologically dated tree, such a rate change is highly improbable.

The challenges of collecting and sequencing *Cantuaria* made obtaining a large dataset difficult; many locations where *Cantuaria* had previously been found did not appear to contain any populations, and collecting locations were vague (e.g. a chalk hill in Canterbury). Some areas were difficult to access for collecting purposes (e.g. Stephen's Island). I was therefore unable to collect specimens from every known population of *Cantuaria*. However, I did discover new populations, and obtained a comprehensive dataset which is representative of the genus.

This study found discordance between individual gene trees (Figs 2–4). For example, in the CO1 phylogeny, specimens from Alexandra and Otago (ID numbers ST1 and SN4–6) form a sister clade to most of the rest of the genus *Cantuaria*. However, in the H3 phylogeny, the Otago specimens SN4–6 form a clade that is only sister to one small clade, containing four sequences.

Discrepancies between gene trees are expected, but may be caused in part by violation of the assumptions made by the Yule prior. The Yule prior is not normally appropriate for analyses involving many sequences per species if there is more than one species (Esselstyn et al. 2012), although it is not violated in the *BEAST analyses which are designed to construct species trees from multiple sequences per species (Heled & Drummond 2010). Despite discrepancy between individual genealogies, the *huttoni* group is consistently recovered as sister to the rest of the genus, including in the *BEAST species tree.

Mapping the phylogeny shows that the genus may have first colonised the southernmost parts of the South Island (Southland and Fiordland) before dispersing to Otago, moving up through Canterbury, and finally into the North Island. Evidently, some lineages may have broken the trend of gradual movement; the D'Urville Island population, for example, is inferred to be basal to some of the South Island clades (Figs. 5.6, 5.9). However, this placement in the phylogeny is not as well-supported as the *huttoni* placement. There is a small possibility that further collection and sequencing would recover the D'Urville population in another clade. A little discordance between node distances and geographic distances is to be expected, partly due to the variability in posterior probability of the geotree (Fig. 5.6), indicating that some of the nodes may be misplaced. True discordance might be explained by chance events that may have occurred in the past 15–18 million years, such as storms washing individuals into the ocean and then back to shore in another location. Males searching for females may also have travelled further than usual, possibly aided by wind, water, or even incidental phoresy. Such events would be extremely rare, but over such a long timescale they would still have an effect on the distribution patterns of the genus. Human interference may also have played a part; for example, a population in Yaldhurst was discovered on a walnut orchard which had imported clay from Cashmere (11 km away). The burrows were only found in and adjacent to the imported clay, leading to speculation that this population had been translocated as a subset of the original population in Cashmere. Yaldhurst specimens were found to be very closely related to specimens from Cashmere, although inferences cannot be made based on their MRCA node because it had low posterior support. Habitat data were not collected from both populations. However, such an example illustrates the possibility that clay or stone could be moved around New Zealand, carrying *Cantuaria* individuals with it. Clay soils that are useful to humans are often inhabited by *Cantuaria*. Verbal evidence from quarriers and road workers, particularly from Christchurch and Charleston, suggests that *Cantuaria* were often unearthed during their work. The fact that *Cantuaria* are found in areas where soil and rocks are removed and transported to other locations may be a strong explanatory factor for closely related individuals being found far apart.

The research presented in this chapter supports the low dispersal ability observed in *Cantuaria* (Irish 2001) and in other closely related mygalomorphs (Arnedo & Ferrández 2007; Starrett & Hedin 2007). The genus has moved across New Zealand primarily by slow dispersal from south

to north, according to phylogeographic analyses of multilocus sequence data. Molecular clocks dated using general mygalomorph substitution rates suggest that *Cantuaria* arrived in New Zealand as recently as 15–18 mya, postdating the emergence of New Zealand from the ocean after the Oligocene drowning. The large rafts of vegetation that occasionally wash to shore from Australia to New Zealand may have harboured a small population of the *Cantuaria* lineage, which then diverged and diversified into the large number of species and forms observed today. The dated phylogeny also divides the West Coast *Cantuaria* clade from the East Coast clades by ca. 8 my, raising the possibility that the rise of the Southern Alps ca. 5 mya may have influenced the structure of the phylogeny by creating an elevation barrier between the two sides of the South Island. There is plenty of scope for the collection of more sequence data, perhaps aided by next-generation sequencing or genomics to design more suitable primers, to study at a higher resolution the patterns of dispersal and vicariance that have shaped New Zealand's trapdoor spider genus.

Chapter 6
The taxonomy of the genus *Cantuaria* Hogg, 1902

6.1 Introduction

The genus *Cantuaria* is New Zealand's only representative of its family, Idiopidae. Lack of competition from other idiopids may explain the wide distribution and niche diversity shown by *Cantuaria*. With 42 described species, it is currently the third most speciose of the idiopids (Natural History Museum Bern 2015), despite its inhabiting only the islands of New Zealand. *Cantuaria* displays a huge diversity in form, life history, and burrow type, which is relatively undocumented in other genera inhabiting South America, Africa, and India.

Cantuaria's taxonomic status has frequently been overturned. Originally placed in the genus *Nemesia* (Nemesiidae) by Pickard-Cambridge in 1878, some species were moved into the genus *Arbanitis* by Simon in 1892. Subsequently, *Cantuaria* spp. have been moved between different genera within the Idiopidae and Ctenizidae, including *Maoriana* and *Korua* (Forster & Wilton 1968). Todd (1945) considered the species to be split between three genera (*Cantuaria*, *Korua* and *Arbanitis*). Forster placed all 42 species, including newly described species, within the genus *Cantuaria* in the family Ctenizidae (Forster & Wilton 1968), but the genus was then synonymised with *Hermeas* within the family Idiopidae by Raven (1985). Subsequently, *Cantuaria* was referred to as within the genus *Misgolas* (Forster, Forster & Otago Museum 1999; Irish 2001), before Raven and Wishart (2005) restored the genus to *Cantuaria* within the family Idiopidae.

In addition to the uncertainty behind the name and placement of the genus *Cantuaria*, there is much uncertainty regarding taxonomic groups and species statuses within the genus. It was haphazardly split into two ecotypes, the *huttoni* group (13 spp., Fig. 6.1B-C), and the non-*huttoni* group (29 spp., Fig. 6.1A) by Forster (1968). Species within the *huttoni* group are generally small; the largest, *C. borealis* (Forster, 1968), is only 10.5 mm long. They build burrows without a lid (although the southernmost species build a lid-like flap), inhabit southern moist bush and forested areas, and the females have dome-shaped spermathecae. Non-*huttoni* species are much larger, usually at least 15 mm long, but the largest, *C. johnsi* (Forster, 1968), can grow up to 30 mm long (pers. obs.). They generally build burrows with lids, although *C. wanganuiensis* (Todd, 1945) and *C. parrotti* (Forster, 1968) do not. Species in the non-*huttoni* group do not live south of Central Otago, and they inhabit a wide variety of environments, from semi-arid banks in Central Otago to West Coast rainforest. The females have elongated spermathecae with bulb-shaped tips. The form of the male palp is also consistently shorter and stouter in the *huttoni* ecotype. While Forster (1968) described 13 different species within the *huttoni* group, Irish (2001) considered them all to be synonymous with *C. huttoni* (O. Pickard-Cambridge, 1880); however, Irish had little taxonomic training. Forster (1968) described 36 new species,

some of which had previously been considered synonymous with already described species (e.g. *C. huttoni;* Irish 2001). Forster (1968), Irish (2001), and Vink, Paquin and Duperre (2010) all considered that the genus *Cantuaria* may in fact be several genera. Raven (Pers. comm.) considers that there may be many more species than described, and that morphology is probably conservative.

Forster (Forster & Wilton 1968) gives detailed descriptions of *Cantuaria* anatomy, and notes on their ecology, to justify taxonomic placement and identification of specimens. Additionally, notes on supposed evolutionary relationships are included; for example, Forster (1968) places 34 of the species into ten separate clades (including a "*dendyi* clade" and a "*johnsi* clade") based on morphology (see Table 6.1). Most of the morphological characters used to distinguish between clades and species involve the genitalia, particularly the shape of the spermathecae in females, and the cymbium in males. However, dorsal patterning, tarsal claws, and the presence or absence of spines on leg segments are also considered important by Forster (Forster & Wilton 1968). Male *Cantuaria* have processes (called spurs) on the tibia of their first pair of legs, which appear to be made up of several short, stout, heavily sclerotised spines; there is little variation in spur form, and the number of sclerotised spines may vary, but Forster (Forster & Wilton 1968) considered the form of the spur to be of "considerable value" in diagnosing species.

Table 6.1: Taxonomic groupings hypothesised by Forster (1968)

Clade name	Species included by Forster (1968)
dendyi	*C. dendyi, C. sinclairi, C. reducta, C. kakahuensis, C. cognata*
myersi	*C. myersi, C. wanganuiensis, C. stephenensis, C. insulana*
gilliesi-depressa	*C. gilliesi, C. depressa, C. lomasi*
unnamed (1)	*C. vellosa, C. grandis, C. maxima, C. aperta*
unnamed (2)	*C. magna, C johnsi, C. prina, C. secunda*
unnamed (3)	*C. marplesi, C. toddi, C. kakanuiensis*
unnamed (4)	*C. huttoni, C. borealis*
unnamed (5)	*C. orepukiensis, C. minor*
unnamed (6)	*C. sylvatica, C. catlinensis*
unnamed (7)	*C. collensis, C. alani, C. delli*

Raven (pers. comm.) relies almost exclusively on male palp morphology for species diagnosis. Raven considers that female morphology cannot be used reliably to diagnose individual species, and considers a female to be the same species as a particular male specimen if characters such as abdominal colouration and eye pattern is similar to the male's, and if the female is found in the same location as the male.

6.1.1 *Cantuaria* general morphology

Cantuaria vary in size from 7.6 mm to 30.0 mm. They are dark-coloured, brown, grey or black spiders, with setation varying from medium (e.g. in *C. dendyi*) to dense (e.g. *C. vellosa;* Forster, 1968). The abdomen often carries chevrons or other patterning, but may be patternless. Maxillae have red lateral fringes. Female *Cantuaria* spp. have dense tarsal scopulae on the palps and first and second pairs of legs, and dense metatarsal scopulae on the first and second pairs of legs. Spinnerets are held tucked underneath the body in life, although when preserved they become extended.

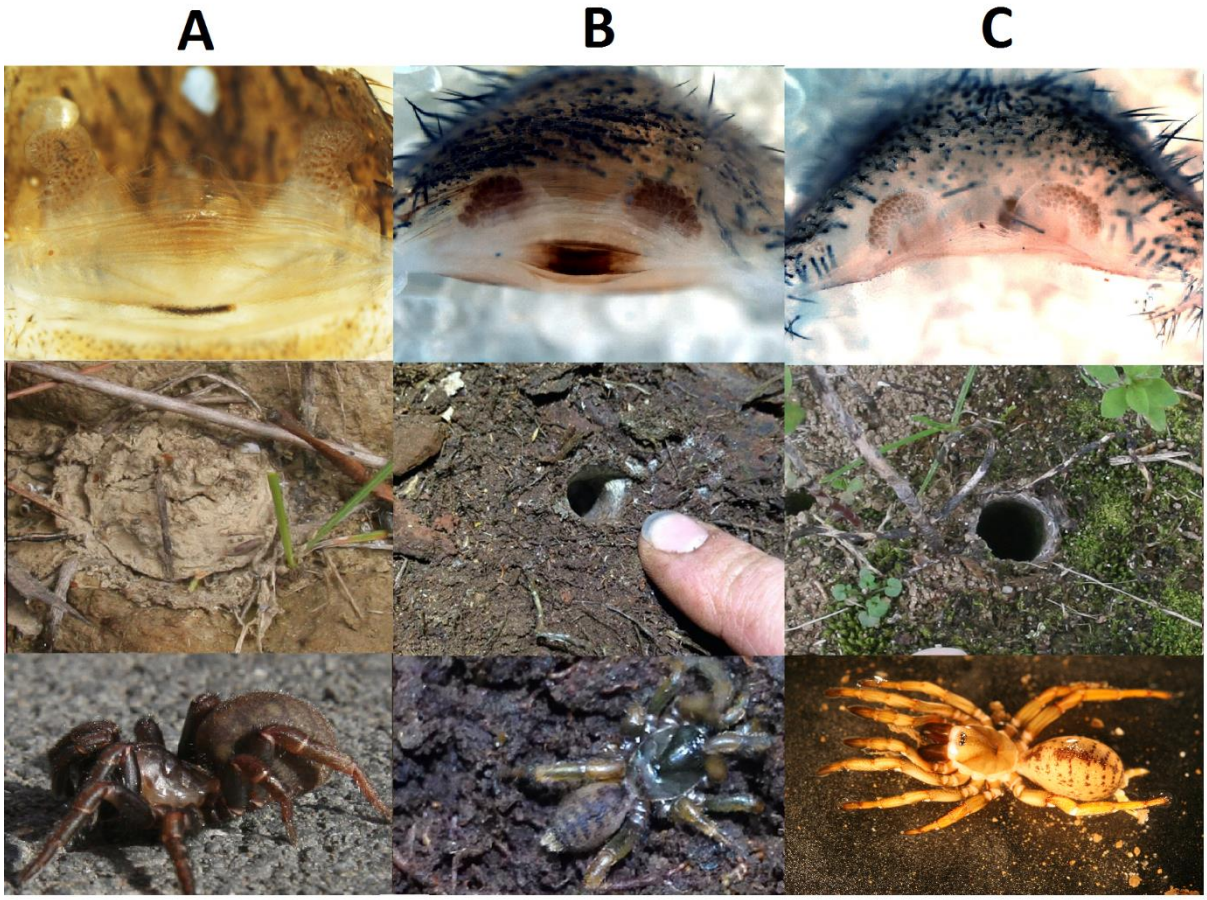

Figure 6.1: Ecotypes within the genus *Cantuaria*, defined by their genitalia (first row), burrow lid type (second row), and morphology (third row). Column A shows non-*huttoni* type *Cantuaria*, while columns B and C show *huttoni*-type *Cantuaria*.

The current study addresses the paucity in taxonomic attention surrounding the genus *Cantuaria* by exploring the phylogenetic structure of the genus, and describing possible new species, using molecular data to inform its conclusions.

The research presented in this chapter aims to explore the taxonomy of the genus *Cantuaria*, including describing any new species that may be found.

6.2 Methods

Holotypes and paratypes held at Otago Museum and the Natural History Museum of London were examined under a dissecting microscope to compare diagnostic features with Forster's (1968) description and illustrations. Particular emphasis has been placed on the form of the male and female genitalia (Forster & Wilton 1968; Raven, pers. comm.). Tibial spurs of males, presence or absence of spines on leg segments, and abdomen patterning was also examined. Other specimens held at Otago Museum that had been examined by Forster, and diagnosed as a particular species, were also examined, photographed, and compared with their descriptions to investigate the degree to which individual morphology may vary. Where tarsal claws were difficult to photograph clearly, drawings were made while examining the specimen.

Specimens were examined and photographed under a Nikon SMZ25 stereomicroscope, except for specimens from the Otago Museum collection (see Appendix C) which were photographed using a non focus-stacking dissecting microscope (model unknown). Specimens were placed in silicon sand and 90% ethanol, or KY- jelly, for ease of manipulation. Where required, body parts such as male palps or legs were excised to expose important structures. Female genitalia were dissected from the abdomen using a hypodermic needle, and soaked in 10% potassium hydroxide until obscuring tissue had dissolved (usually 24 hours).

To further explore the degree of variation within species, individuals were collected from locations specified by Forster (1968), and additional populations were discovered from which individuals were also collected. Females were extracted from their burrows using a tethered beetle (Chapter 4; Smith et al. 2015), and males were collected using pitfall traps. Additional male specimens were obtained from members of the public. Specimens were examined and photographed, and their morphology compared to descriptions by Forster (Forster & Wilton 1968) to diagnose species and assess variation within populations.

To resolve phylogenetic relationships, genomic DNA was extracted using the Qiagen DNeasy Blood and Tissue Kit (Qiagen, Valencia, CA, USA) or ZR Genomic DNA™-Tissue MiniPrep (Zymo Research) kit, and individual gene phylogenies were constructed using BEAST (A. Drummond & Rambaut 2007) (see Chapter 5). A multi-locus phylogeny was also constructed using *BEAST (Drummond et al. 2005). Relationships shown by all phylogenies were compared to Forster's theoretical taxonomic groupings (Table 6.1), and species groupings.

6.2.1 Species delimitation

In this taxonomic study, I implement the phylogenetic species concept, which defines a (sexual) species as the "Smallest aggregation of populations [...] diagnosable by a unique combination of character states in comparable individuals" (Nixon & Wheeler 1990). Using a combination of characters is preferred over a single non-homoplasious autapomorphy, as variation within a species may mean that some individuals do not exhibit all characters. Further, the phylogenetic species concept takes the dynamic process of speciation into account, while making species easy to diagnose based on characters (Nixon & Wheeler 1990).

A Poisson tree process analysis (PTP) (Zhang et al. 2013) was conducted to guide species delimitation based on phylogenetic relationships shown by individual gene trees. The PTP method, in contrast to the widely-used general mixed Yule coalescent (GMYC) method of species delimitation, does not require an ultrametric tree input. The PTP has been shown to be a more robust and consistent implementation of phylogenetic species delimitation than GMYC (Tang et al. 2014; Zhang et al. 2013) and is more resistant to unresolved nodes or other artefacts of discrepancies between gene trees (Tang et al. 2014). Final species delimitation was based primarily on phylogenetic relationships, which have previously proven reliable in mygalomorphs (Bond & Hedin 2006; Bond et al. 2012; Hamilton et al. 2011; Hendrixson & Bond 2007) and may in some taxa be more informative than morphology, which can be highly conserved (Bond et al. 2001; Hamilton et al. 2011; Starrett & Hedin 2007).

While PTP is a reliable method of species delimitation, it may be prone to overestimating the number of species, particularly when using mitochondrial data (Hamilton et al. 2011). A combined approach was therefore used, delimiting new species based largely on phylogenetic relationships and PTP species delimitation, but incorporating geographic location and morphological data. Individual species resembling Forster's (1968) descriptions in terms of geographic (type) location and general morphology were considered to be those species. Where a species was delimited by the PTP, it also had to be morphologically distinctive or found in a new location for it to be considered a distinct species. Species found in type locations that were genetically different from species more closely resembling Forster's (1968) description were also considered new species. Speciation was generally assumed to be dominated by allopatric speciation, as geographical barriers appear to be important in segregating *Cantuaria* clades (see Chapter 5); however, sympatric speciation was not ruled out as a possibility. Where two sister species were morphologically very similar and found in the same location, but differed genetically enough for the PTP to delimit them as separate species, they were considered the same species.

New species were described following Forster's (1968) methods to give the general impression of the appearance of the individuals. Morphological descriptions should be interpreted with the knowledge that there is extensive morphological variation and polymorphism in this genus (see

Section 6.3: Results). Species were described based on the type material. Preliminary assessment of characters determined that maxilla, labia and chelicerae morphology did not appear to show enough variation between species to be useful taxonomic characters, so these were omitted from descriptions. Spinneret morphology was also excluded from species descriptions; preservation in ethanol causes spinnerets to expand, so that preserved specimens have different spinneret morphology from live specimens. Spinneret morphology is therefore unlikely to be of taxonomic value in diagnosing species. However, for the benefit of future research, spinneret morphology is included as Appendix E. The most important part of the description, that should be used for diagnosis, is the genetic sequence description. However, general appearance and geographic location can be used as an indicator of species if DNA sequencing facilities are not available.

6.3 Results

Seventy-six locations were searched (see Fig. 6.2) and 226 *Cantuaria* specimens were obtained. Specimens were collected from as far south as Stewart Island, and as far north as Whanganui. Every effort was made to obtain specimens from throughout *Cantuaria*'s range, including remote locations such as Whero Rock, in order to represent the genus as comprehensively as possible. While female specimens were easy to find and catch using beetling (Smith et al. 2015), males were much more difficult to find. However, 15 male specimens were collected from pitfall traps and members of the public making up 6.6% of the total sample set. These freshly collected specimens were used for phylogenetic analysis (see Section 6.3.2: Phylogenetics).

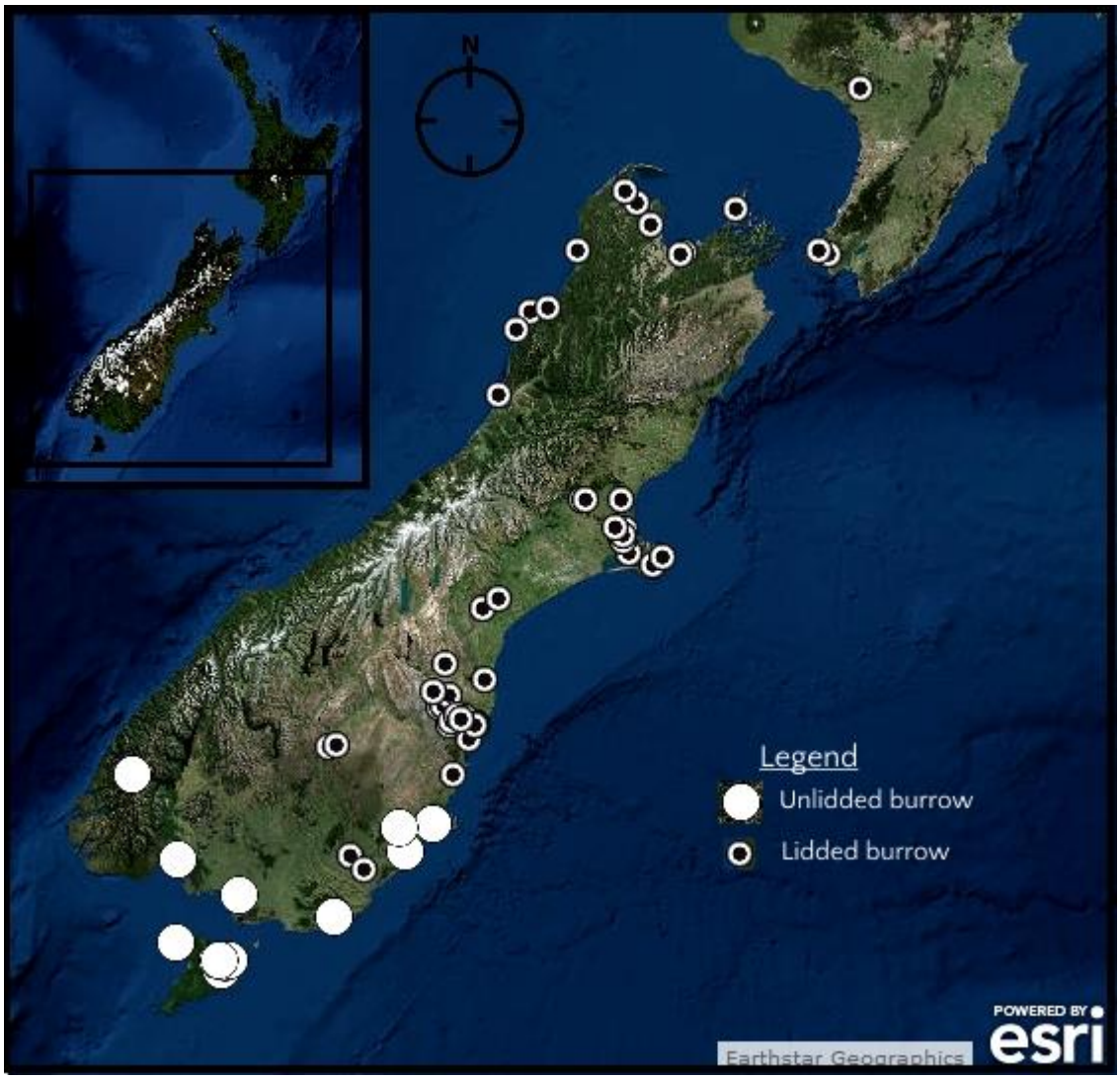

Figure 6.2: Locations where *Cantuaria* spp. were found and obtained for taxonomic analysis.

In addition to the material previously mentioned, six specimens from the Natural History Museum in London, 16 specimens from the Lincoln University Entomology Museum, and 29 specimens from Otago Museum (including holotypes of already described species) were examined (see Appendix C). Of these, 33 were males.

While identifying individuals to species level, the characters considered important by Forster (1968) were found to be often polymorphic within a population (or even between left and right sides of an individual). Many characters were also found to be monomorphic across several populations from different areas. Individuals from type locations differed from Forster's (1968) drawings in dorsal patterning, tarsal claws, spurs, and genitalia; sometimes individuals would have characters that matched some aspects of the description, but others that did not. Tarsal claws, genitalia, and spurs often differed between left and right of the same individual (Fig. 6.3). A thorough search for new useful characters was not conducted due to limitations on time and resources. Future research may investigate candidates for taxonomic characters, such as size ratios of different body parts.

Some individuals had genitalia that closely resembled Forster's (1968) drawings of genitalia from individuals found in completely different locations; for example, a specimen found in Christchurch had genitalia resembling *C. napua* (Forster, 1968), a species from Oamaru 200 km away (Fig. 6.5).

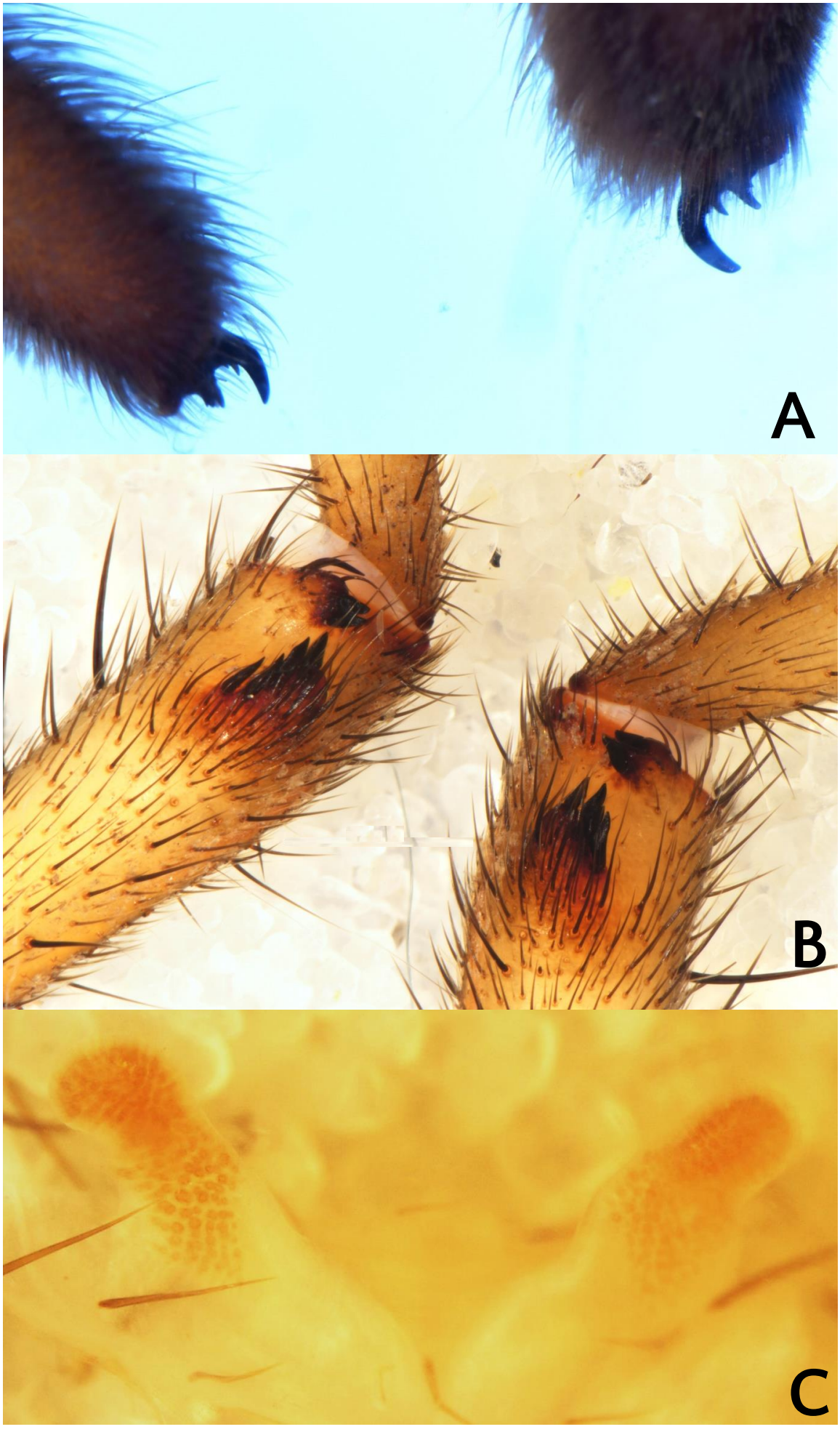

Figure 6.3: Examples of common discrepancies between left and right characters that were previously thought to be diagnostic. Each numbered pair of characters shows the left and right sides of the same individual. A: tarsal claws (note that one claw may have been damaged, which is not a natural discrepancy; the form of the basal tooth, however, is variable); B: spurs (male); C: spermathecae (female).

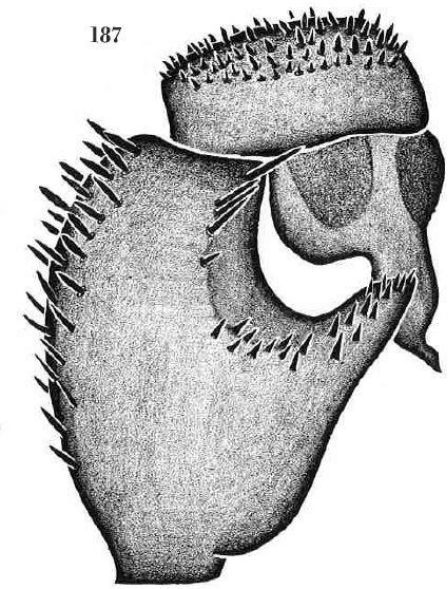

Figure 6.4: The *Cantuaria minor* holotype male palp (left) bears a strong resemblance to the drawing of a *C. minor* palp made by Forster (1968) (right).

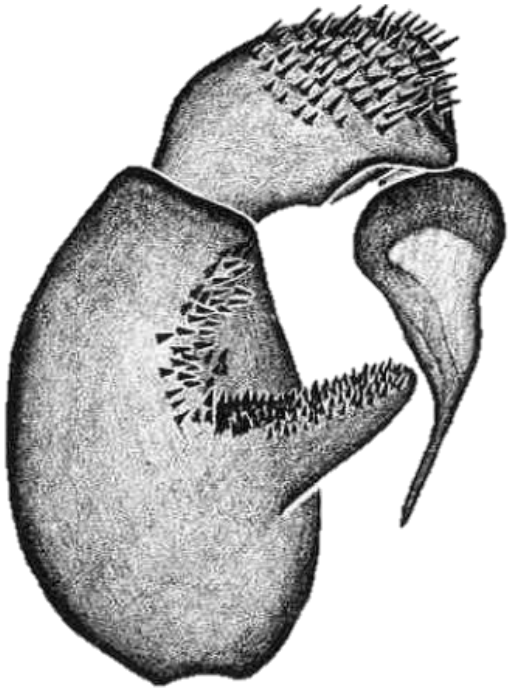

Figure 6.5: The palp of an individual found in clay in Christchurch (left), with genitalia respresenting that of *C. napua* (right; drawing by Forster (1968). Genetic analysis (see phylogeny section) revealed this individual to be within the Christchurch *dendyi* clade.

Most holotypes resembled Forster's (Forster & Wilton 1968) drawings and descriptions closely (Fig. 6.4). However, paratypes and other specimens that had been diagnosed by Forster were often undissected, or their dorsal patterning, tarsal claws, and/or spur form did not match the species descriptions or drawings. Spination on leg segments showed little variation between individuals collected from populations throughout New Zealand.

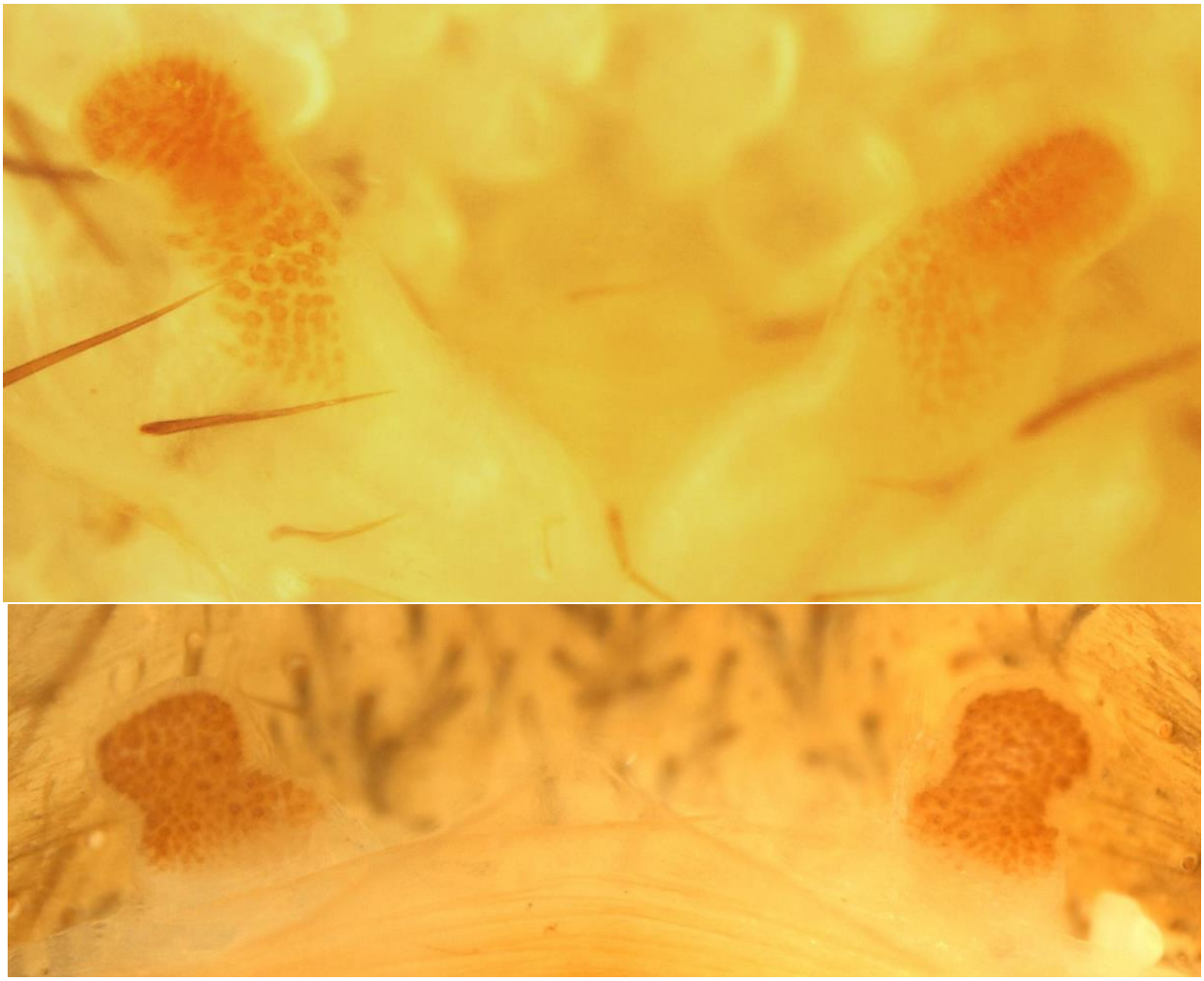

Figure 6.6: Genitalia from two individuals that were both physically and genetically in the same population. The top individual has elongate, rounded spermathecae, while the bottom individual has squat, stout spermathecae that are flattened at the distal edge.

Figure 6.7: Dorsal sides of abdomens from three individuals found from different populations around Christchurch. These individuals were found to be genetically the same species, but abdomen colouration varies, including dark shading with pale patches (left), dark chevrons on a pale background (middle), and a pale abdomen with some dark shading (right).

Overall, there was enormous intraspecific, and even intrapopulation, variation in female genitalia (Fig. 6.6), dorsal patterning (Fig. 6.7), tarsal claws, and spurs (Fig. 6.8). Eye pattern was more consistent between different populations, possibly correlated with species; however, eye pattern was subject to occasional teratogeny (Fig. 6.9). Eye pattern was not formally investigated as useful; character, as eye pattern is generally less reliable than other characters such as genitalia (Wishart 1992). However, examination suggests that there is little variation in eye pattern between individuals from different species. There was insufficient variation in spination to use as a morphological character.

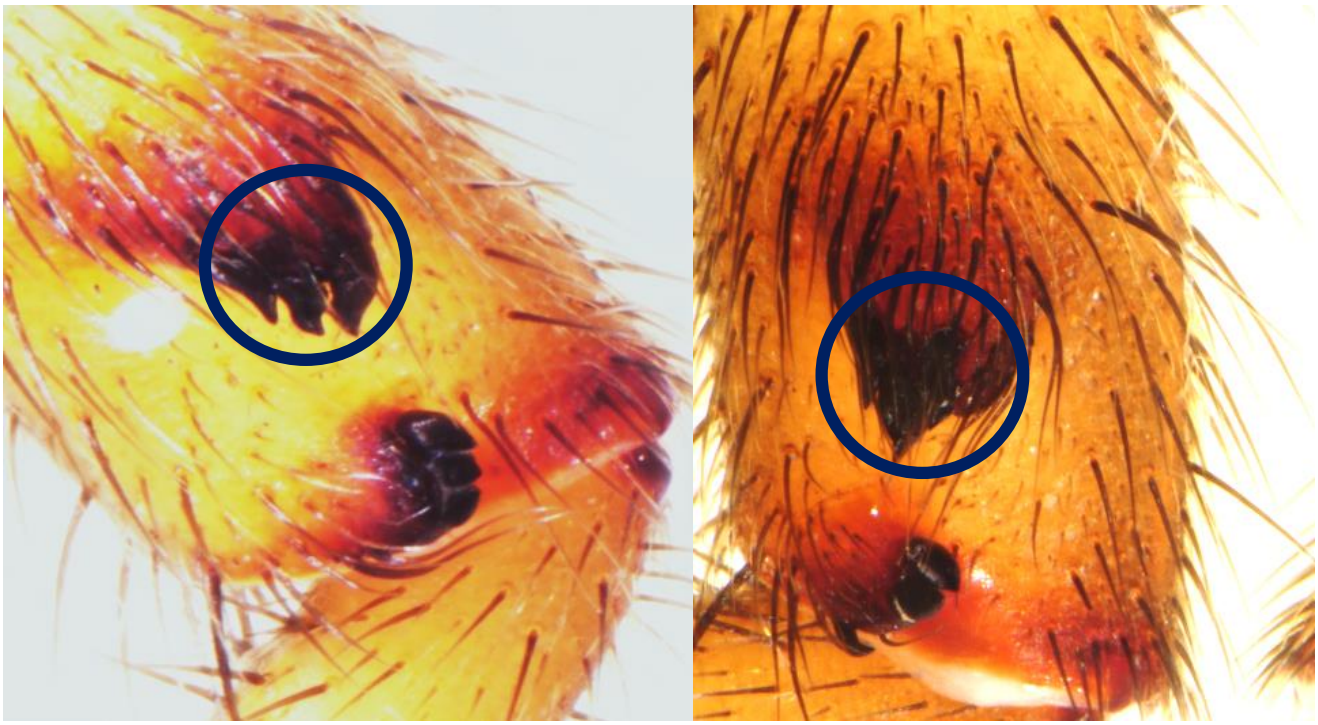

Figure 6.8: Spurs (circled) from two male *Cantuaria* sp. found in the same population. One male (left) has claw-shaped spurs and the other (right) has leaf-shaped spurs. Other males in this population showed variations of claw-shaped and leaf-shaped spurs.

Figure 6.9: Eyegroup of a male *Cantuaria* sp. found in Christchurch. Phylogenetically, this individual is placed within the Christchurch *dendyi* group. This individual is missing its right anterior lateral eye.

6.3.1 Phylogenetics

This chapter focuses on the taxonomy and species delimitation, using phylogenies as a tool. See Chapter 5 for more details concerning the phylogenetic relationships within the genus *Cantuaria.*

Individual gene trees (Figs. 14–16) generally concur that three major monophyletic clades exist. One contains the large species found in the north of the South Island, the West Coast and Central Otago (the "*johnsi* clade", due to the inclusion of *C. johnsi* and the superficial resemblance of the other species to *C. johnsi*). This clade is genetically diverse, with deeply diverging nodes. Another contains the Canterbury *Cantuaria*, comprehensively sampled for this study and named the "*dendyi* clade" due to its inclusion of *C. dendyi* and the superficial resemblance of the other species to *C. dendyi*. A particular individual was given a code depending on where it was collected, presented here as a means of identifying individuals from different areas.

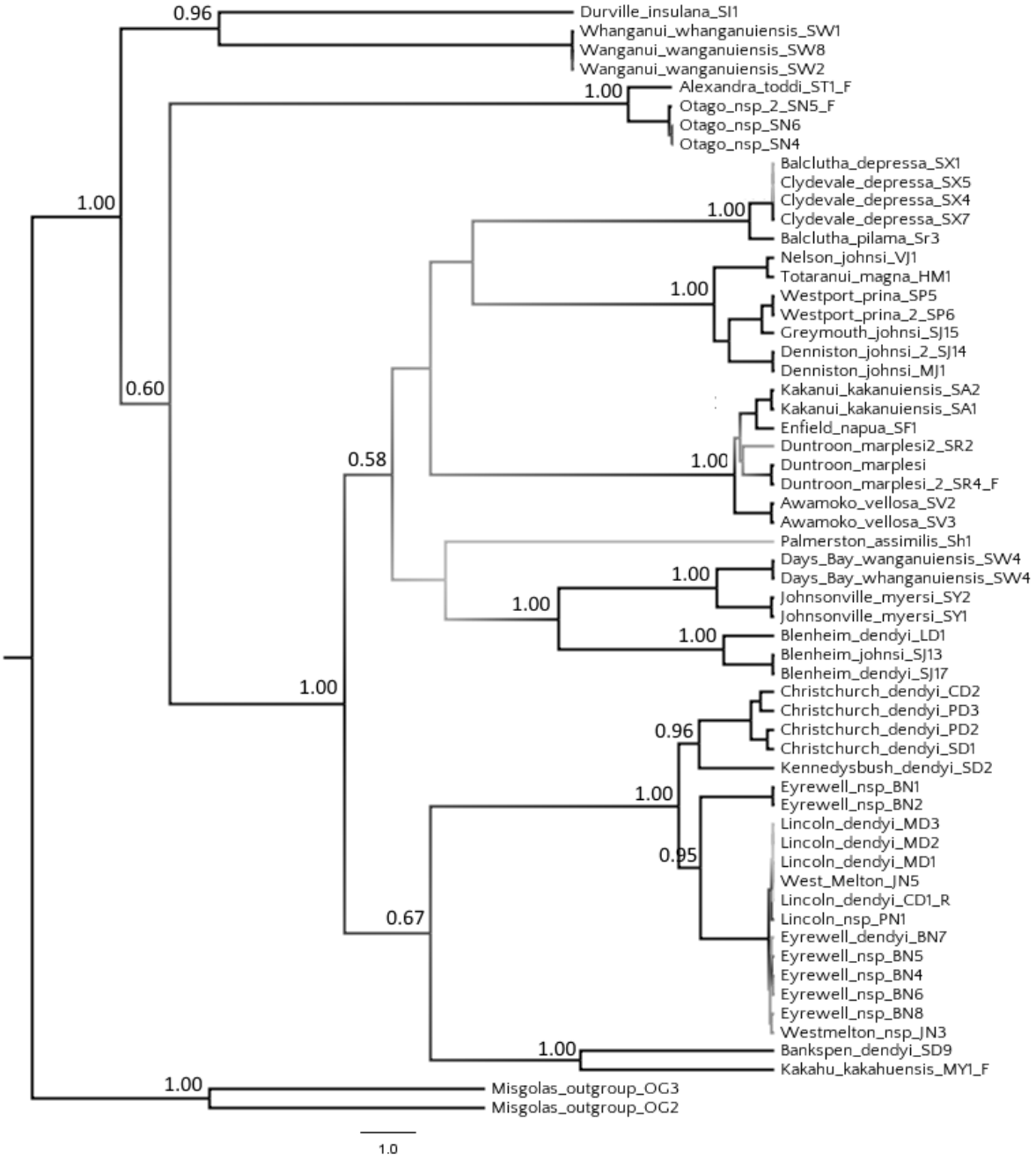

Figure 6.10: CO1 gene tree representing the full sample of specimens collected throughout New Zealand, for which the amplification of CO1 was successful. Darker branches represent higher posterior probabilities, and numbers at nodes indicate posterior probability.

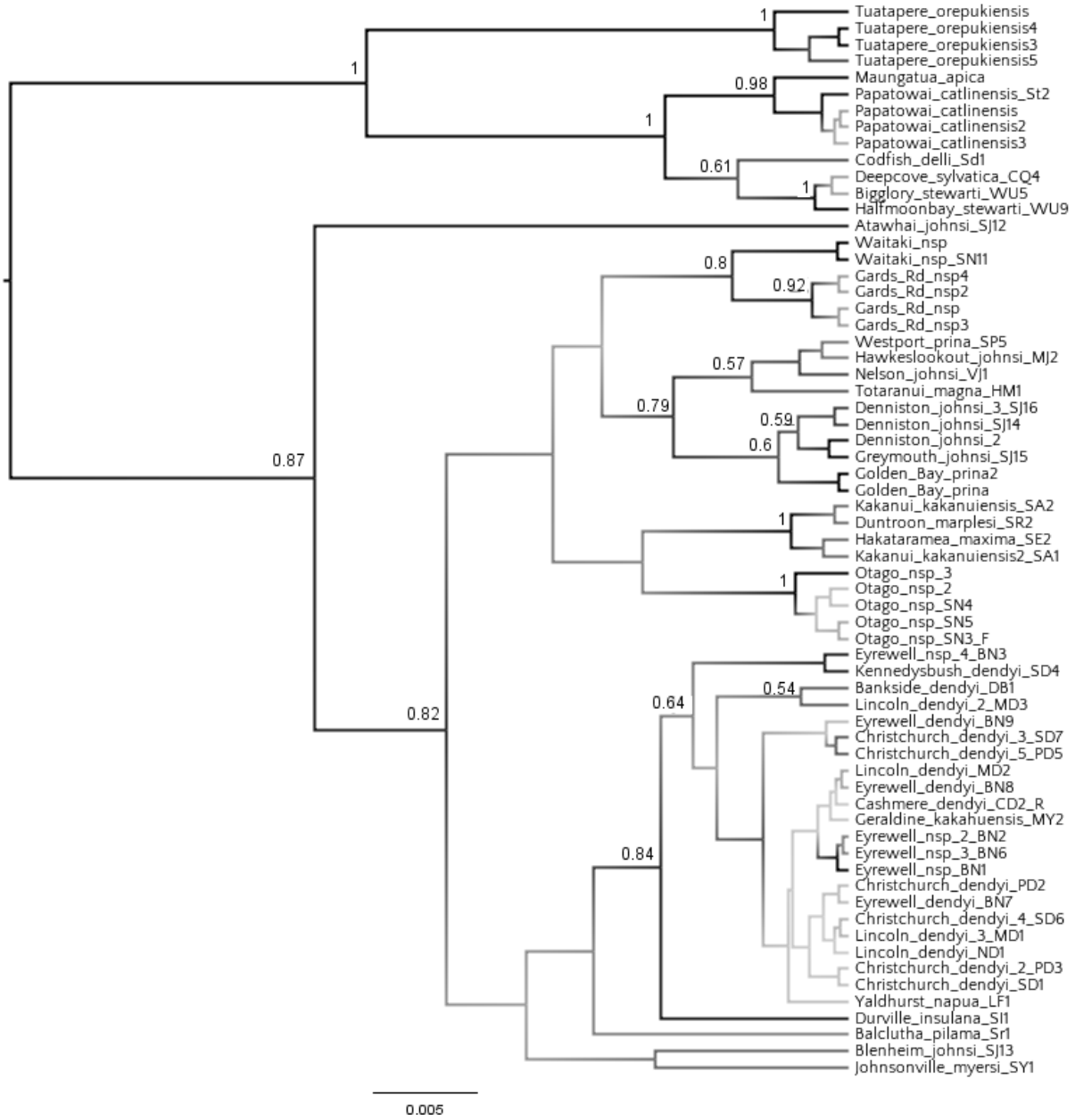

Figure 6.11: H3 gene tree, representing the full sample of specimens collected throughout New Zealand for which the amplification of H3 was successful. Darker branches represent higher posterior probabilities, and numbers at nodes indicate posterior probability.

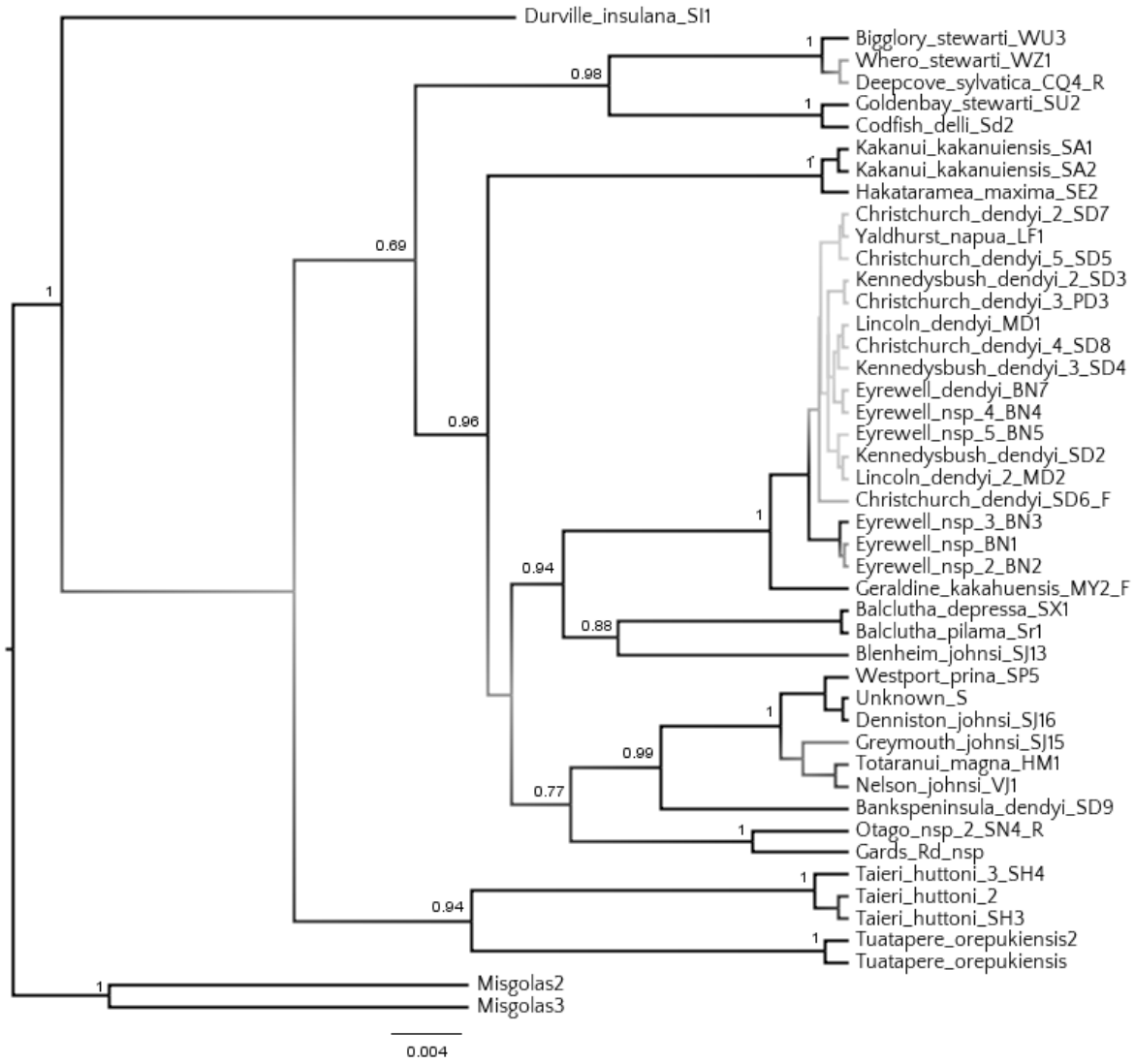

Figure 6.12: ITS gene tree, representing the full sample of specimens collected throughout New Zealand for which the amplification of ITS was successful. Darker branches represent higher posterior probabilities, and numbers at nodes indicate posterior probability.

The third clade, supported by both the H3 and ITS phylogenies (amplification of the members of this clade was not possible for CO1), consisted of all the species referred to by Forster (1968) as the "*huttoni*" group. The ITS phylogeny (Fig. 6.12) split the *huttoni* group into two deeply diverging sister groups, but the split was poorly supported (posterior probability=0.69). The placement of *C. insulana* (found on D'Urville Island) varied between lineages, sometimes being sister to the entire rest of the genus (ITS, Fig. 6.12) but other times being in a clade with other species (CO1, Fig. 6.10). In general, individuals from geographically close locations were found to be phylogenetically close.

The results of the PTP analysis of the whole genus CO1 tree are shown in Fig. 6.18. The phylogenies varied in their ability to be used for PTP analysis due to the differences in evolution rates and posterior probabilities shown between trees. The ITS and H3 trees had low posterior support for some fundamental branches, making the trees difficult to reconcile and less suitable

for PTP analysis than the CO1 trees. Species delimitation was therefore focused on the CO1 tree and subtrees (Figs. 6.17–6.20). Species delimitation attempts for ITS are shown in Fig. 6.17, but few delimitations carried a high enough posterior probability to be considered credible. The ITS and H3 genes evolve more slowly than CO1, which is why CO1 is often used to delimit species (Hamilton et al. 2011; Tang et al. 2014).

The PTP species delimitation was consistent when applied to the whole genus and its parts; higher posterior probabilities were achieved when a single clade was processed as opposed to the whole sample set (Figs. 17–20). Based on collecting location and differences or similarities in morphology, 18 species (including three new species and 15 described species) were believed to have been included in the CO1 phylogeny; however, 30 species were retrieved by the PTP (Figs 14–17). Most species from the same location with similar morphology were included together as one species, matching a name given by Forster (1968). However, some specimens resembled a description based on general morphology and location, but were found to be distantly related to others, which matched the general description and collecting locations for the same species. For example, species resembling *C. johnsi* (Forster, 1968) that were found in locations where *C. johnsi* had been found made up four different species, and were included in some clades with specimens resembling *C. dendyi* (Hogg, 1901). Additionally, the variation in morphology of individuals collected in and around Christchurch, Eyrewell and Lincoln led to assumption that there were two distinct species, and possibly more; however, genetically they are the same species (Fig. 6.14). Identifying an individual down to species will not always be possible without molecular analysis; however, collecting location can be used to infer the most likely clade in which the individual belongs, and morphology may provide further insight into which species the individual is most likely to be.

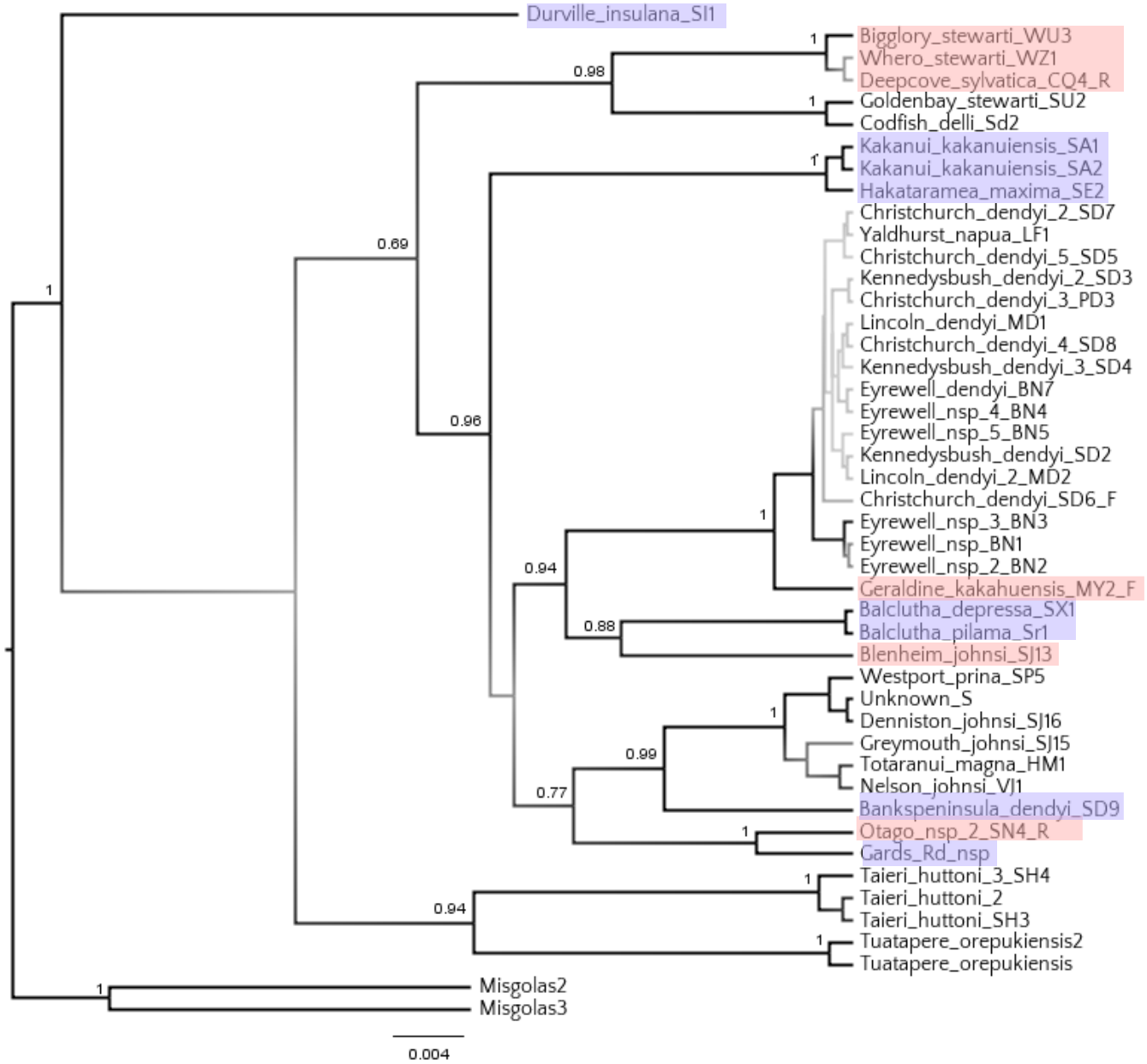

Figure 6.13: Phylogeny of the *Cantuaria* ITS gene. Red and purple boxes show species designations estimated by the PTP with posterior probabilities of >0.8. All other species designations based on the ITS tree have low posterior probabilities.

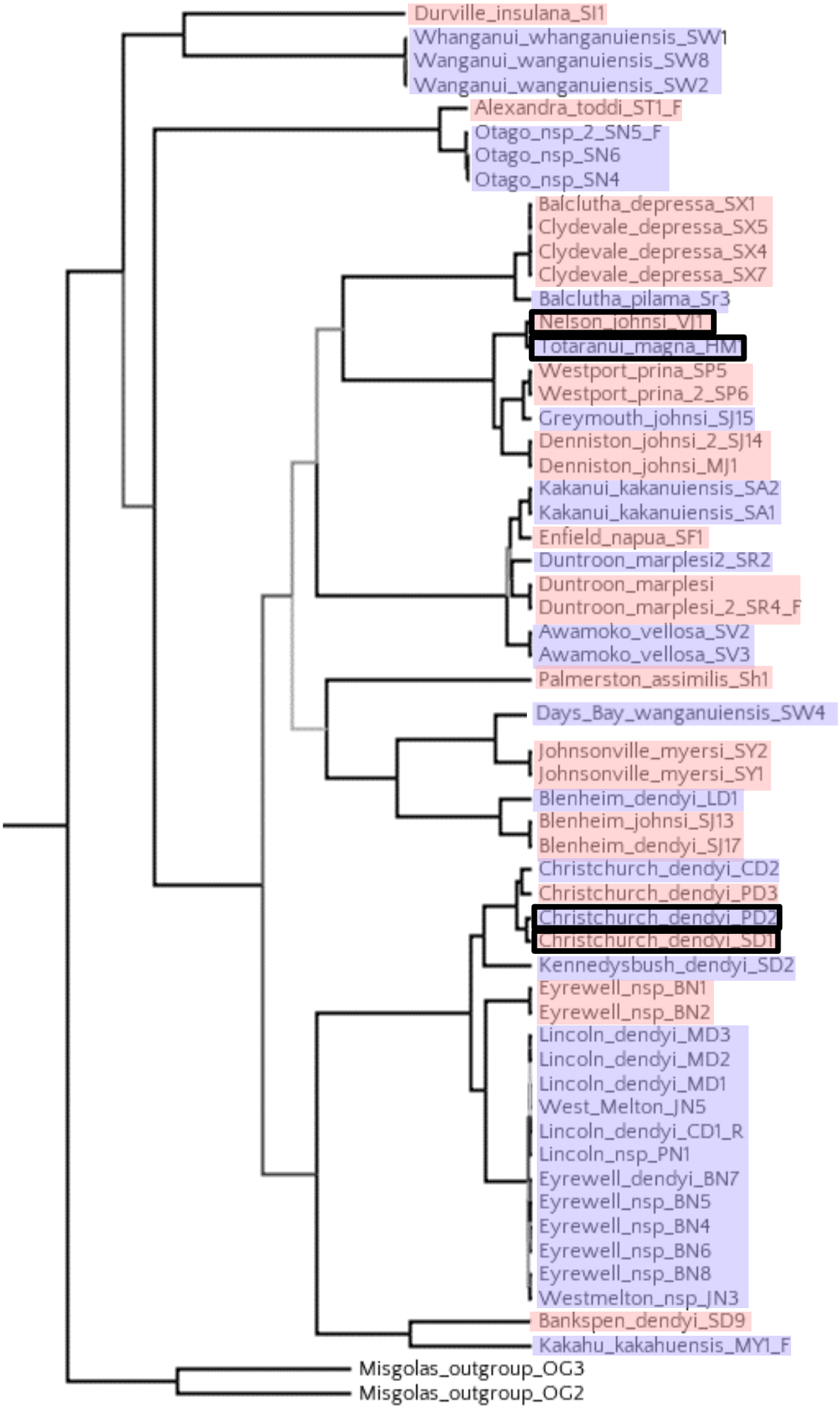

Figure 6.14: Phylogeny of the *Cantuaria* CO1 gene, with the PTP results superimposed as coloured boxes. Tips included inside a single red or purple box are a discrete species, according to the PTP results. Boxes with bold black outlines denote species with low posterior probabilities (<0.8).

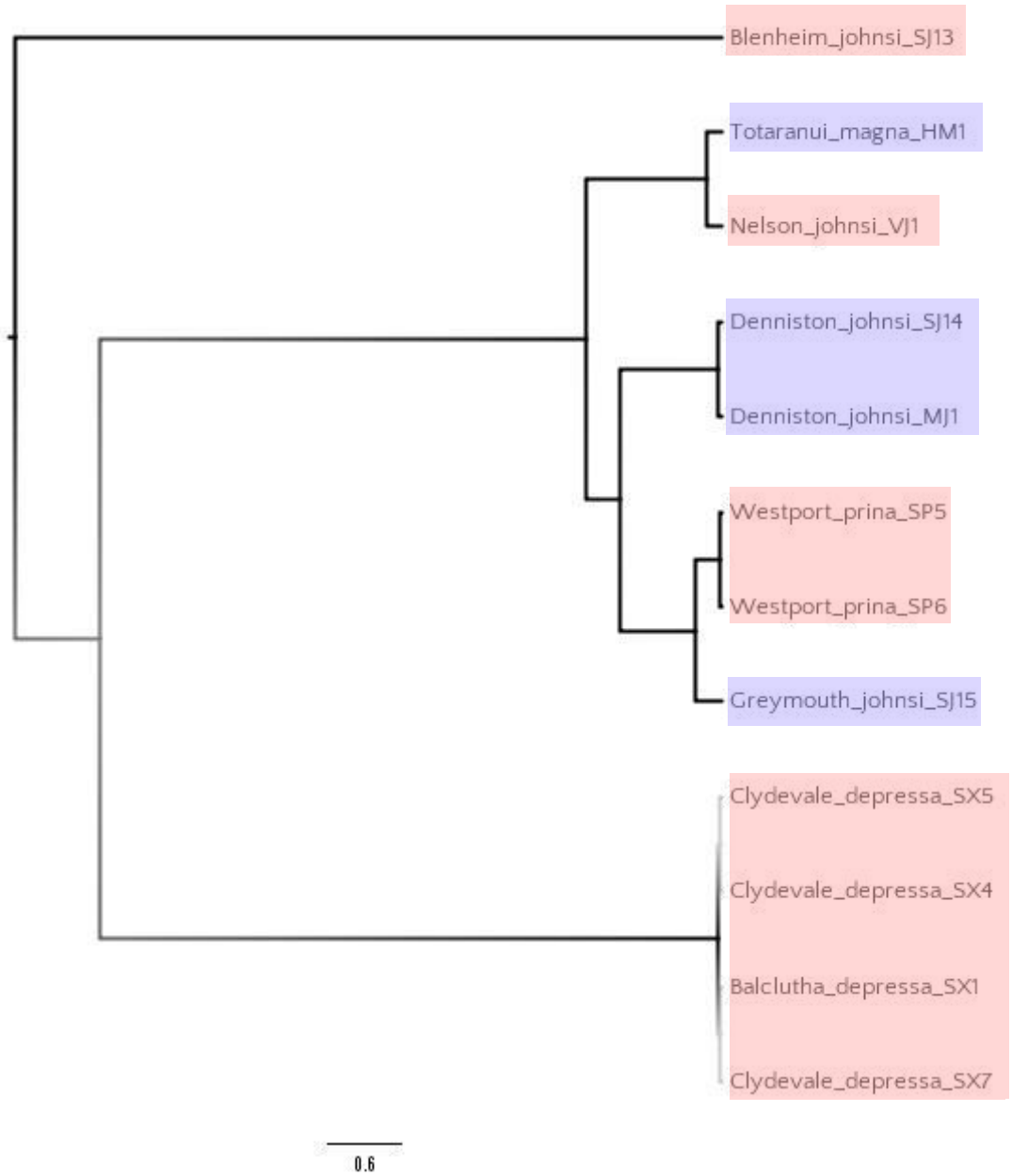

Figure 6.15: A CO1 tree of the *johnsi* clade within the genus *Cantuaria*, showing PTP species delimitation. The grey node as a posterior probability of 0.51; all other nodes have posterior probabilities between 0.99 and 1. All the tips included within a single red or purple box are members of a single species. All posterior probabilities for the PTP species delimitation were >0.8.

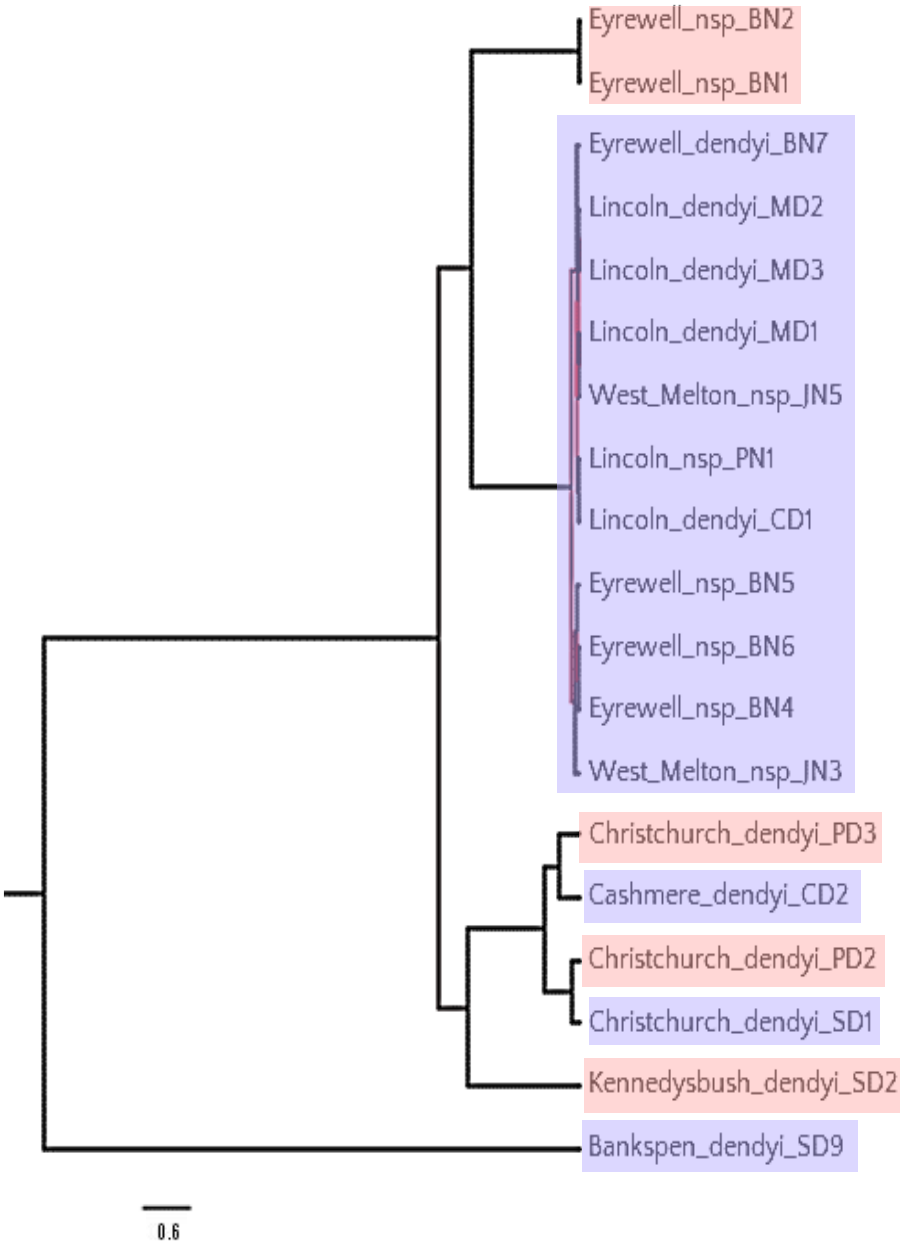

Figure 6.16: Gene phylogeny (CO1) for the *dendyi* clade of *Cantuaria*. Black branches have a posterior probability of 0.95–1.0; red branches have a posterior probability of <0.8. Tips contained within a single red or purple box are retrieved as a single species by the PTP. All PTP posterior probabilities are >0.8.

Poisson tree process delimitation applied to the CO1 gene tree suggests 15 new species additional to the 15 currently recognised species represented by the phylogeny (Figs. 6.14–6.16). I find good evidence for 12 new species when taking morphology and geography into account. Species designations, including new species described in Section 6.3.2, are shown in Fig. 17.

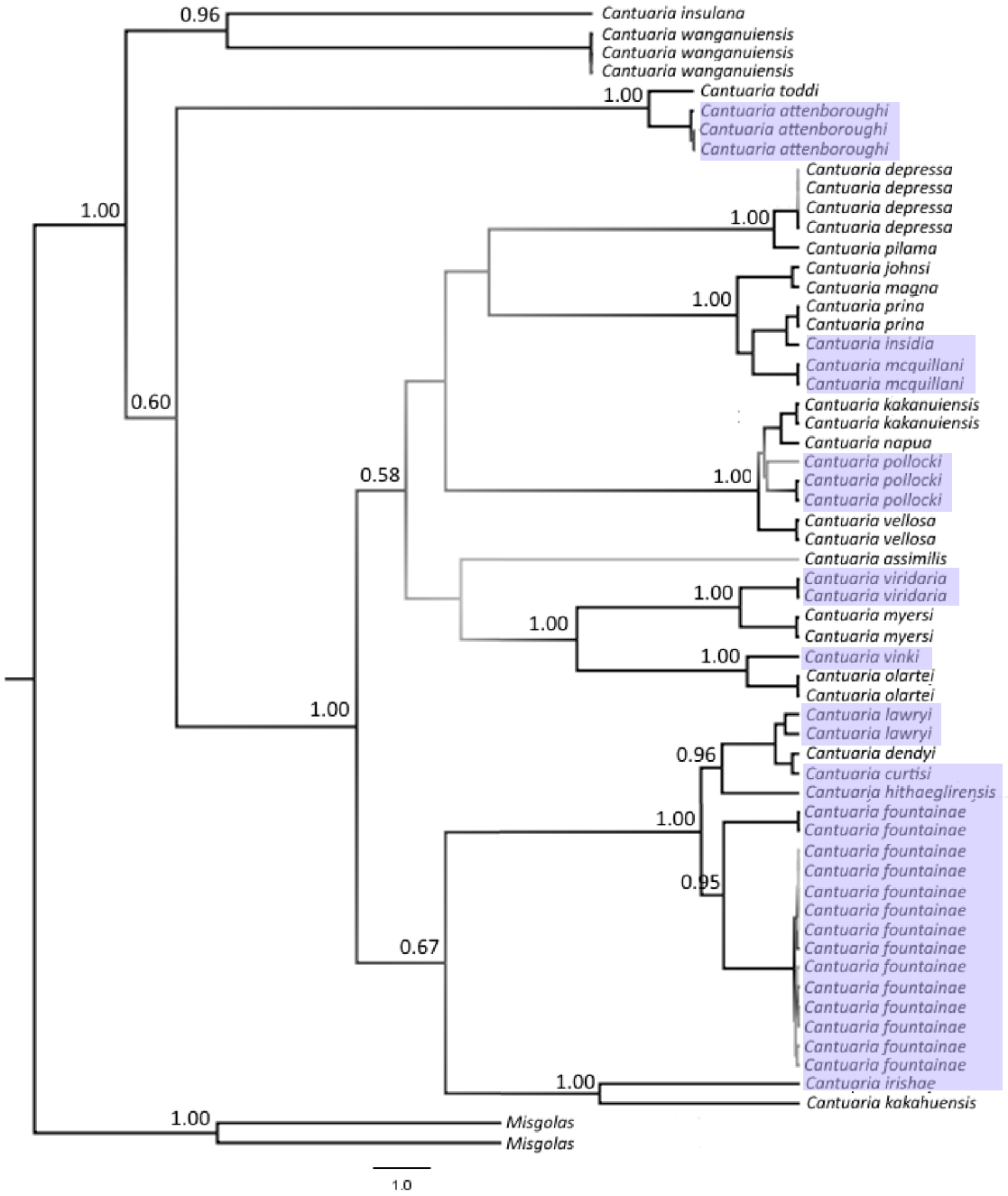

Figure 6.17: Gene phylogeny for CO1 showing species designations, including new species described in this chapter. Numbers at nodes show posterior probabilities, and branches are colour coded with darker branches having higher posterior probabilities. New species are highlighted in blue.

6.3.2 Taxonomy

Family Idiopidae Simon, 1889 (for diagnosis, see Raven 1985)

Subfamily Arbanitinae

Genus *Cantuaria* Hogg, 1902

Maoriana Hogg, 1901 (junior homonym of *Maoriana* Suter, 1891 (Mollusca: Gastropoda))

Arbanitis Hogg, 1901

Cantuaria Hogg, 1902 (neonym).

Arbanitis Hogg, 1902

Cantuaria Simon, 1903

Arbanitis Todd, 1945

Korua Todd, 1945

Synonymised with *Arbanitis* by Parrott (1946)

Synonymised with *Hermeas* Karsch, 1878 (junior synonym of *Misgolas* Karsch, 1878; R. Raven & Wishart 2005) by Raven (1985)

Restored to *Cantuaria* from *Misgolas* by Raven & Wishart (2005)

Removed from synonymy of *Arbanitis* Koch, 1874 by Raven & Wishart (2006)

Type species *Cantuaria dendyi* Hogg, 1901 (original type specimen in the Natural History Museum London).

For description and diagnosis of the genus, see Forster (1968). The first pair of sigillae are not always readily visible, but the form of the female and male genitalia are probably most useful in diagnosing the genus, as discussed by Forster (1968). Time and resources did not allow for a full diagnosis of the genus *Cantuaria*, but future research may find more useful autapomorphies when comparing *Cantuaria* to other idiopid genera.

Cantuaria attenboroughi n.sp.

Fig. 6.18

Diagnosis

This species is smaller than *C. toddi* (for description, see Forster, 1968), with clearer patterning on the dorsal surface of the abdomen, and a distinctive white line running from anterior to posterior on the abdomen. The female spermathecae do not curve at the base as they do in *C. toddi*, and the distal ends of the spermathecae are more bulbous. This species is found off Conroys Road in Central Otago, and may be sympatric with *C. toddi*.

Gene sequences

Cytochrome oxidase subunit 1 sequences from this species were uploaded onto GenBank (see Appendix F). Genetic variation between the 3 specimens tested was less than or equal to 0.3%. *Cantuaria attenboroughii* sequences differed from the sequence in their sister clade (*C. toddi*) by 4.6–4.9%.

FEMALE

Measurements

Carapace length 5.8 mm	width 4.2 mm
Abdomen length 7.3 mm	width 4.6 mm

Colour

Carapace and legs pale creamy beige, darker on the carapace behind the head. Chelicerae dark beige-brown. The abdomen is pale creamy grey with many small dark brown spots forming 5–7 thin recurved lines. Some lines are broken. There is a white median stripe running from anterior to posterior, breaking up the markings. Ventral surface is pale beige and covered with fine, soft hairs, but no markings.

Carapace

Fovea deep, dark, long and straight.

Eyes

The eyegroup occupies 6/19 of the width of the head. Viewed dorsally, the anterior row is slightly procurved and the posterior row is slightly recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 62:38.

Sternum

Longer than wide in the ratio 15:11. The posterior pair of sigillae is slightly wider than the median pair; sigillae are only faintly visible.

Palp

Tarsus with thick scopula. Metatarsus with scopula on the distal edge, fading towards the proximal edge. Claw with two strong basal teeth, the proximal of which is bifid; two smaller teeth are found approximately midway along the claw.

Legs

Legs 1 and 2 with a thick scopula on the tarsi and metatarsi. Superior claws of leg 1 with a strong tooth at the base which is bifid medially. A smaller tooth is located approximately midway along the claw.

Spinnerets

The lateral pair are longer than the medial pair in the ratio of 35:6.

Material examined

Holotype female. In semi-arid patch of private land off Conroy's Road S45°16'28.6" E169°20'06.4", Central Otago, April 2014, V. Smith (Canterbury Museum), beetled out of a lidded burrow.

Paratype female. In semi-arid patch of private land off Conroy's Road S45°16'28.6" E169°20'06.4", Central Otago, April 2014, V. Smith (Natural History Museum London), beetled out of a lidded burrow.

Paratype female. In semi-arid patch of private land off Conroy's Road S45°16'28.6" E169°20'06.4", Central Otago, April 2014, V. Smith (Canterbury Museum), beetled out of a lidded burrow.

Paratype female. In semi-arid patch of private land off Conroy's Road S45°16'28.6" E169°20'06.4", Central Otago, April 2014, V. Smith (Canterbury Museum), beetled out of a lidded burrow.

Paratype female. In semi-arid patch of private land off Conroy's Road S45°16'28.6" E169°20'06.4", Central Otago, April 2014, V. Smith (Canterbury Museum), beetled out of a lidded burrow.

Etymology

This species is named after Sir David Attenborough in recognition of his contribution to inspiring my career, science in general, and zoology in particular.

Species notes

This species is plentiful in the semi-arid patches of habitat near Conroy's Road. It inhabits dry, sandy soil and builds tightly-fitting lids, sometimes in the middle of a patch of *Raoulia* (vegetable sheep) with some of the plant forming the lid. In all specimens that were found, the white stripe down the median dorsal surface of the abdomen is present. The form of the genitalia is particularly variable in this species. It is morphologically very different from *C. toddi*, its closest relative.

Figure 6.18: *Cantuaria attenboroughii* (female only). A) habitus dorsal B) habitus ventral C) spermathecae D) first leg claw E) palpal claw F) eye group.

Cantuaria curtisi n.sp.
Fig. 6.19

Diagnosis

This species is most closely related to *C. dendyi* (see Forster 1968 for description). The abdomen is more heavily pigmented in *C. curtisi*, and the posterior median eyes are closer together. The form of the claws also differs. Only one population of this species is known, but there are probably more in the immediate area, near Cashmere in Christchurch.

Gene sequences

Cytochrome oxidase subunit 1 sequences from this species were uploaded onto GenBank (see Appendix F). *Cantuaria curtisi* sequences differed from the sequence in their sister clade (*C. dendyi*) by 0.7%.

SUBADULT FEMALE

Measurements

Carapace length 9.7 mm	width 7.2 mm
Abdomen length 12 mm	width 8.5 mm

Colour

Carapace and legs yellow-gold with grey-brown patches near the edge of the carapace. Chelicerae dark brown. The abdomen is pale creamy beige with dark brown spots forming thick lines that become contiguous as they reach the lateral edges. Ventral surface of the abdomen is pale brown with a broad dark brown median patch tapering towards the spinnerets. The ventral surface of the prosoma is pale brown with a thin covering of short dark brown hairs.

Carapace

Fovea long, dark and very slightly procurved.

Eyes

The eyegroup occupies 19/45 of the width of the head. Viewed dorsally, the anterior row is slightly procurved and the posterior row is slightly recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio 4:3.

Sternum

Equally long as it is wide. The posterior pair of sigillae is slightly larger than the median pair.

Palp

Tarsus with thick scopula. Claw with a strong basal tooth proximal to a small tooth near the base.

Legs

Legs 1 and 2 with a weak scopula on the tarsi. Superior claws of leg 1 with a strong tooth near the base which is bifid proximally.

Spinnerets

The lateral pair are longer than the medial pair in the ratio of 16:3.

Material examined

Holotype subadult female. In clay bank along Hoon Hay Valley Road S 43°35'38.1" E 172°36'15.0", Canterbury, March 2014, V. Smith (Canterbury Museum), beetled out of a lidded burrow.

Female paratypes from the same population with similar morphology. In clay bank along Hoon Hay Valley Road (S 43°35'38.1" E 172°36'15.0"), Canterbury, December 2014, V. Smith (Canterbury Museum), beetled out of lidded burrows.

Etymology

This species is named after ecologist Nathan Curtis for his help, support and friendship throughout this project.

Species notes

This species is aggressive. Despite the small genetic difference between *C. curtisi* and *C. dendyi*, they are recovered as different species by the PTP, and they differ morphologically. The two species are also found in different areas of Christchurch. Further collecting may reveal morphological differences to be part of the pattern of variation within *C. dendyi*, but based on the evidence collected for this thesis, *C. dendyi* and *C. curtisi* are considered different species.

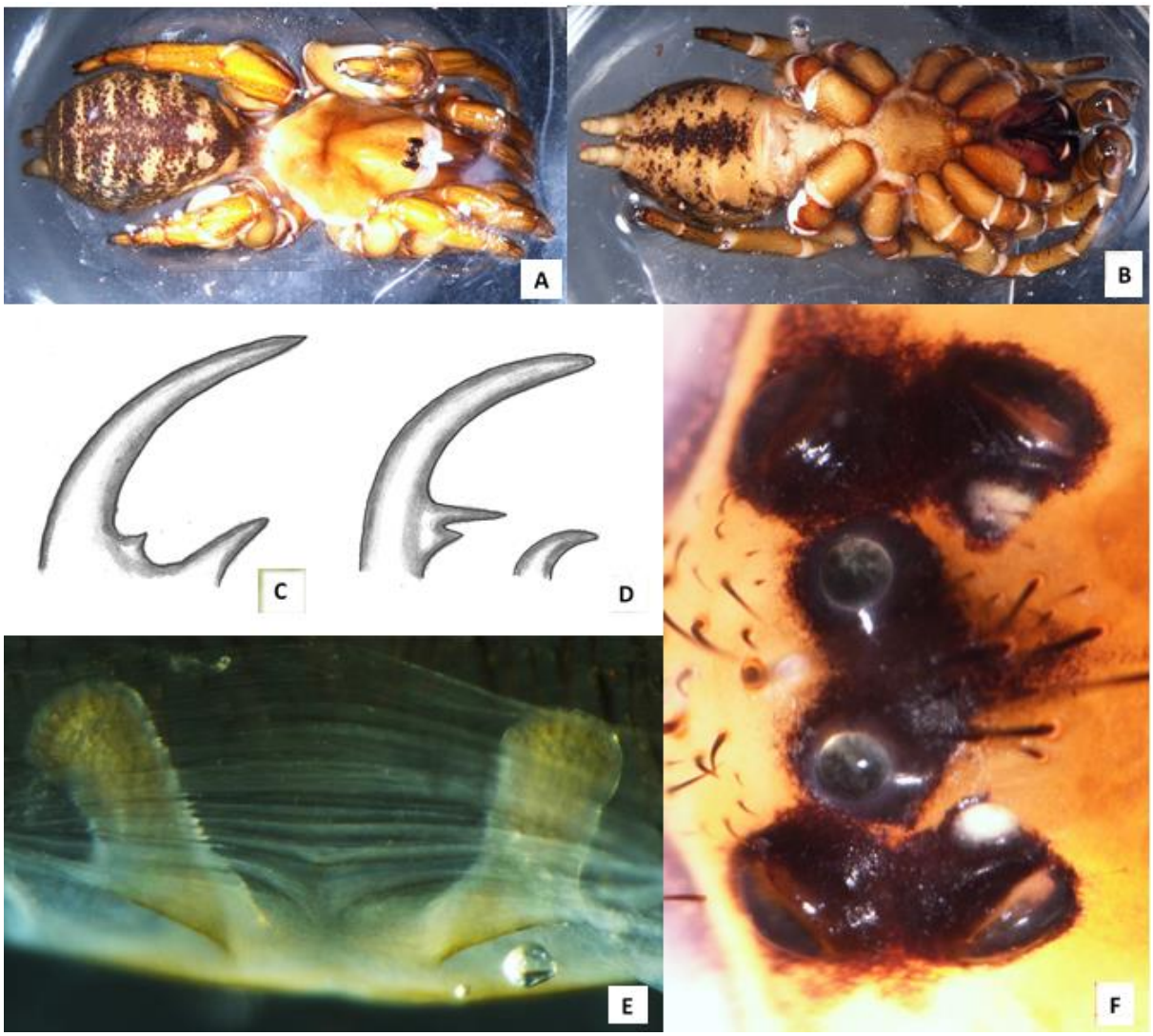

Figure 6.19: *Cantuaria curtisi* (female only). A) habitus dorsal B) habitus ventral C) palp claw D) first leg claw E) genitalia (taken from a paratype) F) eye group.

Cantuaria fountainae n. sp.

6.20

Diagnosis

Abdomen is pale and lightly patterned, not heavily shaded as in closely-related spiders. Spermathecae angled at about 45 degrees to the epigynum, unlike *C. curtisi* n.sp. or *C. lawryi* n. sp. which have spermathecae angled closer to 90 degrees to the epigynum. The sclerotised nodules of the spermathecae run to the base of each spermatheca, unlike *C. curtisi*, *C. dendyi*, or *C. lawryi*. The male embolus is short, and the bulb is a stout triangle, unlike *C. dendyi*'s long, tapered bulb. The bifurcated tooth in the superior tarsal claw of the first leg is distinct from the single strong tooth of *C. hithaeglirensis* n. sp., and the spermathecae are more heavily sclerotised in *C. fountainae* than *C. hithaeglirensis*. *Cantuaria fountainae* has a wide distribution around Christchurch and its outer suburbs.

Gene sequences

Cytochrome oxidase subunit 1 sequences from this species were uploaded onto GenBank (see Appendix F). Genetic variation between 11 of the 13 specimens tested was less than or equal to 0.4%. The remaining two specimens (designated as a separate species by the PTP, but considered the same species when taking morphology and geography into account) differed from the other *C. fountainae* specimens by 7.2%. *Cantuaria fountainae* sequences differed from sequences in their sister clade by 7.3-9.9%.

Description

MALE

Measurements

Carapace length 6.2 mm	width 5.2 mm
Abdomen length 5.5 mm	width 3.9 mm

Colour

Carapace pale creamy yellow with brown streaks outlining the head. Chelicerae and legs a light brown. The abdomen is a pale creamy yellow with a wide dark brown median band, and between five and seven broken lateral branches. Ventral surface pale with dark patches and a dark band between the epigastric groove and the spinnerets.

Carapace

Fovea straight or slightly recurved. Lateral margins with 1–2 rows of small bristles. Striae with shorter, finer bristles than those on lateral margins.

Eyes

The eyegroup occupies 1/3 of the width of the head. Viewed dorsally, the anterior row is slightly procurved and the posterior row is slightly recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 17:13.

Sternum

Longer than wide in the ratio 17:16. Coxae 4 contiguous.

Palp

The bulb is short and stout, tapering in a triangle to the base of the thin distal portion, which is kinked in two places and points ventrally at the tip. Short spines on the tarsus with three long spines on the distal edge. Between two and three rows of short, stout spines line the edge of the tibial depression.

Legs

Weak scopula on the tarsus of leg 1. Superior claws on the first pair of legs with one tooth at the base, which is bifid proximally. Spurs leaf-like.

Spinnerets

The lateral pair are longer than the medial pair in the ratio of 37:12.

FEMALE

Measurements

Carapace length 9.0 mm	width 6.6 mm
Abdomen length 10.9 mm	width 7.7 mm

Colour

Carapace and legs pale cream, with dark brown shading on the carapace posterior to the head and orange shading in the centre of the carapace. Chelicerae dark brown. The abdomen is pale cream with many small dark brown spots forming five recurved lines. Ventral surface of the abdomen is pale with a wide median dark patch, tapering towards the spinnerets. Ventral surface of the prosoma is dark brown.

Carapace

Fovea deep and slightly procurved. Lateral margins with 1–2 rows of setae.

Eyes

The eyegroup occupies 9/35 of the width of the head. When viewed dorsally, the anterior row is slightly procurved and the posterior row is slightly recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 7:5.

Sternum

Longer than wide in the ratio 4:3. The posterior and median pairs of sigillae are approximately the same size.

Palp

Tarsus with thick scopula. Metatarsus with scopula. Claw with a strong basal tooth.

Legs

Leg 1 with a thick scopula on the tarsi and metatarsi. Leg 2 with thick scopula on the tarsi and distal half of the metatarsi. Superior claws of leg 1 with a tooth at the base which is bifid proximally.

Spinnerets

The lateral pair are longer than the medial pair in the ratio of 3:1.

Material examined

Holotype male. Eyrewell, Canterbury, July 2014, M. Bowie (Canterbury Museum), caught in pitfall trap. Allotype female. Lincoln, Canterbury, March 2014, S. Moore (Canterbury Museum).

Lincoln, Canterbury, caught in pitfall trap, April 2014, D. Leeh (Canterbury Museum). Lincoln, Canterbury, two female specimens, March 2014, S. Moore (Canterbury Museum).

West Melton, Canterbury, two male specimens. March and July 2014, P. Johns (Canterbury Museum).

Lincoln, Canterbury, June 2012, C. B. Phillips (Canterbury Museum).

Coordinates for these specimens are not recorded.

Etymology

This species is named after Dr. Emily Fountain for her large contribution towards this research and the beginning of my scientific career.

Species notes

This species appears to inhabit a range of habitats throughout Canterbury. It has been caught in pitfall traps, and dug from burrows on many occasions. The burrows are sometimes unlidded, particularly when found under logs.

Figure 6.20: *Cantuaria fountainae*. Male: A) habitus dorsal B) habitus ventral C) first leg claw D) spurs E) palp F) eye group. Female: A) habitus dorsal B) habitus ventral C) first leg claw D) palp claw E) spermatheca F) eye group.

Cantuaria hithaeglirensis n.sp.

Fig. 6.21

Diagnosis

This species is most closely related to *C. lawryi*, *C. curtisi*, and *C. dendyi* (see Forster 1968 for description). It has more complex abdominal markings than any of these three. Its spermathecae resemble curved match heads. The posterior lateral eyes are 2.25 times larger than the posterior median eyes: a larger order of magnitude than any of the closely related species. *Cantuaria hithaeglirensis* is found in Kennedy's Bush.

Gene sequences

A CO1 sequence from this species was uploaded onto GenBank (see Appendix F). DNA sequences could only be obtained from one individual, but the CO1 sequence differed from sequences in its sister clade (*C. lawryi*, *C. curtisi*, and *C. dendyi*) by 7.5–7.8%.

FEMALE

Measurements

Carapace length 7.4 mm	width 6.1 mm
Abdomen length 8.2 mm	width 6.3 mm

Colour

Carapace and legs yellow-brown. Chelicerae deep brown. The abdomen is grey-brown, with dark brown-black patterning and spots in the form of patches and broken lines. Ventral surface of the abdomen is pale creamy grey with dark brown median triangular patches and a few small dark brown lateral patches. Ventral surface of the prosoma is yellow-brown with a sparse covering of brown hairs.

Carapace

Fovea thin and slightly procurved.

Eyes

The eyegroup occupies 23/70 of the width of the head. Viewed dorsally, the anterior row is slightly procurved and the posterior row is slightly recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 4:3.

Sternum

The sternum is as wide as it is long.

Palp

Tarsus with thick scopula, metatarsus with weak scopula. Claw with a strong basal tooth and a smaller tooth proximal to the mid point.

Legs

Legs 1 and 2 with a thick scopula on the tarsi. Leg 1 with a weak scopula on the distal portion of the metatarsi. Leg 2 with a thick scopula on the distal portion of the metatarsi. Superior claws of leg 1 with a small tooth proximal to a strong tooth at the base.

Spinnerets

The lateral pair are longer than the medial pair in the ratio of 47:8.

Material examined

Holotype female. Kennedys Bush, clay bank beside track through native forest S 43°37'33.4"S E 172°37'23.9". March 2014, V. Smith (Canterbury Museum), caught by beetling from lidded burrow.

Paratypes female (two individuals). Kennedys Bush, clay bank beside track through native forest. March 2014, V. Smith (Canterbury Museum), caught by beetling from lidded burrow. S 43°37'33.4" E 172°37'23.9"

Etymology

The species is named after Hithaeglir, the Misty Mountains from Tolkein's Middle Earth. The specimens used in this description were obtained after many hours of driving and walking in thick mist in the Port Hills, reminding the author of Tolkein's descriptions of Hithaeglir in The Hobbit.

Figure 6.21: ***Cantuaria hithaeglirensis*** **(female only). A) habitus dorsal B) habitus ventral C) genitalia D) first leg claw E) palp claw F) eye group.**

Cantuaria insidia n.sp.

Fig. 6.22

Diagnosis

One of the largest species of *Cantuaria*, this species closely resembles the smaller *C. prina* (see Forster 1968 for description) both morphologically and genetically. However, it is found in a different geographic location (Greymouth). Its abdominal markings are faint, but stronger than those described for *C. prina*; the ventral side of the abdomen is unmarked but has a uniform dense covering of dark brown hairs, unlike *C. prina* which has a pale ventral surface with a dark longitudinal band. The claw has small, distinct teeth rather than one large bifid tooth as in *C. prina*. The spermathecae of *C. insidia* are longer and less rounded than *C. prina*.

Gene sequences

A CO1 sequence from this species was uploaded onto GenBank (see Appendix F). Only one individual could be found, but the sequence differed from its sister species (*C. prina*) by 1.8%. The two *C. prina* specimens did not differ from each other. The small genetic difference between *C. insidia* and *C. prina* may be a symptom of recent speciation; *C. prina* and *C. insidia* have different geographic ranges and different morphology, and are therefore considered here to be different species.

FEMALE

Measurements

Carapace length 12.7 mm width 10.4 mm

Abdomen length 14.2 mm width 10

Colour

Carapace and legs a deep red-brown, paler on the carapace behind the head. The eyegroup is surrounded by a deep orange-red. Chelicerae dark brown-black. The abdomen is covered with fine dark beige-brown hairs, with a pale cream anterior median patch, and faint dark brown patterning. Ventral surface of the abdomen is pale orange-yellow with a dense covering of long dark brown hairs. Ventral surface of the prosoma is dark red-brown with dense black hairs.

Carapace

Fovea deep and straight. Lateral margins with a row of fine setae.

Eyes

The eyegroup occupies 8/25 of the width of the head. Viewed dorsally, the anterior row is procurved and the posterior row is recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 19:14.

Sternum

The posterior part of the sternum has been misplaced in error in the type specimen.

Palp

Tarsus with thick scopula. Metatarsus with scopula. Claw with a strong basal tooth which is bifid subapically on the proximal edge. Three smaller teeth are present near the base but distal to the bifid basal tooth.

Legs

Legs 1 and 2 with a thick scopula on the tarsi and metatarsi. Superior claws of leg 1 with a strong tooth at the base and another smaller tooth proximal to the midpoint.

Spinnerets

The lateral pair are longer than the medial pair in the ratio of 62:17.

Material examined

Holotype female. Greymouth, Westland, S42°28'31.9" E171°11'10.8", September 2014, V. Smith (Canterbury Museum), caught by beetling in daylight from lidded burrow in heavily disturbed clay bank.

Etymology

This species is named after Insidia, the ancient Roman personification of ambush. During daylight hours, the author was walking by a clay bank when the type specimen leapt at high velocity from its burrow, apparently reacting to the presence of the author.

Species notes

Only one *C. insidia* individual was found despite extensive searching. The habitat surrounding the burrow of this adult female was heavily developed with housing and landscaping and it is possible that the type specimen was the last surviving individual in her population. Any further populations of this species that may be found in the future must be protected, as the species may be at risk.

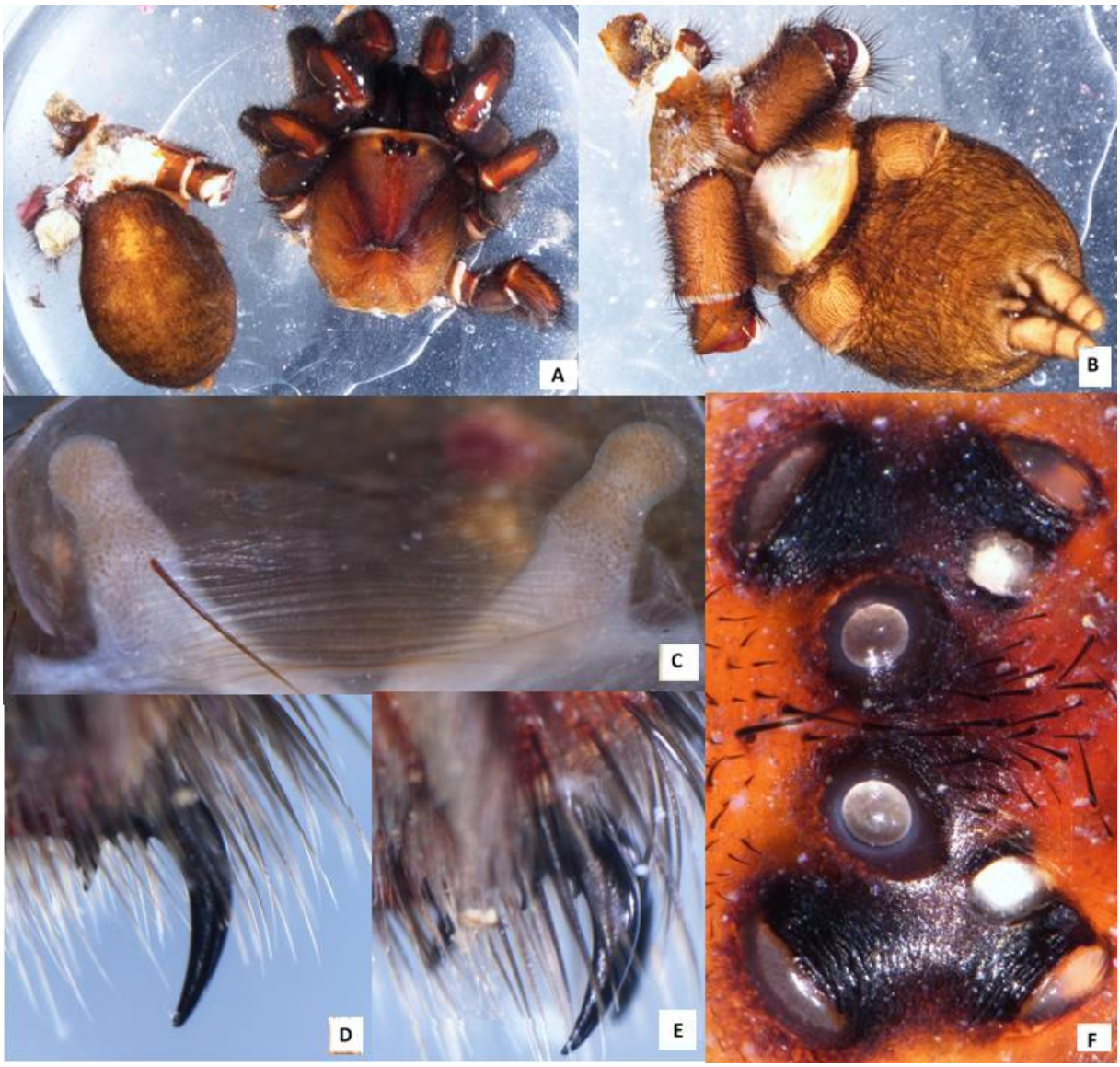

Figure 6.22: ***Cantuaria insidia*** **(female only). A) habitus dorsal B) opisthosoma ventral C) spermathecae D) palp claw E) first leg claw F) eye group.**

Cantuaria irishae n.sp.
Fig. 6.23

Diagnosis

This species is most closely related to females found in Kakahu that may be *C. kakahuensis*. The palp claw of *C. irishae* has a strong basal tooth that is not present in the Kakahu females. The first leg claw has two teeth proximal to the midway point that are not present in the Kakahu females. *Cantuaria irishae* is also much larger than the Kakahu females. However, they are otherwise morphologically very similar and may only be reliably differentiated by geographic location (*C. irishae* is found in Le Bons Bay while the Kakahu females were found in Kakahu).

Gene sequences

Cytochrome oxidase subunit 1 sequences from this species were uploaded onto GenBank (see Appendix F). The *C. irishae* sequence differed from the sequence in its sister clade (females from Kakahu) by 14.5%.

FEMALE

Measurements

Carapace length 9.5 mm width 7.7 mm

Abdomen unknown

Colour

Carapace and chelicerae a deep red-brown. legs grey-brown and yellow-brown, Two dark streaks outline the head and there is one grey quadrangles either side of the eye group. Abdomen yellow-brown with darker grey-brown patterning which is not visible in the type specimen. Ventral surface of the prosoma is yellow-brown and covered with brown-black hairs.

Carapace

Fovea dark and straight.

Eyes

The eyegroup occupies 16/47 of the width of the head. Viewed dorsally, the anterior row is slightly procurved and the posterior row is slightly recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 4:3.

Sternum

Longer than wide in the ratio 83:72. The sigillae are only faintly visible.

Palp

Tarsus with thick scopula. Claw with three small teeth proximal to the midpoint, and a strong basal tooth.

Legs

Legs 1 and 2 with a thick scopula on the tarsi. Leg 1 with a thick scopula on the metatarsi. Leg 2 with a thick scopula on the distal portion of the metatarsi. Superior claws of leg 1 with a strong tooth at the base which is bifid proximally. Two smaller teeth are located proximal to the midpoint.

Material examined

Holotype female. In roadside bank outside Le Bons Bay School, S43°45'37.5" E173°03'13.3", Banks Peninsula, October 2014, V. Smith (Museum of New Zealand), beetled out of a lidded burrow in daylight.

Etymology

This species is named after the late Lindsay Irish for her passion for *Cantuaria* and contribution to trapdoor spider research.

Figure 6.23: ***Cantuaria irishae*** **(female only). A) habitus dorsal B) habitus ventral C) palp claw D) first leg claw E) eye group.**

Cantuaria lawryi n.sp.

Fig. 6.24

Diagnosis

This species is most closely related to *C. curtisi* and *C. dendyi* (see Forster 1968 for description). The ventral side of the abdomen is almost entirely shaded in *C. lawryi*. rather than having only a median patch. The spermathecae stand upright or at a slight angle, rather than curving or pointing to the sides. The form of the claw and number of claw teeth is also different. *Cantuaria lawryi* is found in rural Christchurch near the Port Hills (Cashmere area), and shares its range with *C. dendyi* and probably also *C. curtisi*.

Gene sequences

Cytochrome oxidase subunit 1 sequences from *C. lawryi* were uploaded onto GenBank (see Appendix F). The two *C. lawryi* sequences differed from each other by 2.1%. *Cantuaria lawryi* sequences differed from the sequence in their sister clade (*C. dendyi* and *C. curtisi*) by a minimum of 2.8% and a maximum of 7.1%.

FEMALE

Measurements

Carapace length 9.2 mm	width 6.7 mm
Abdomen length 8.5 mm	width 4.8 mm

Colour

Carapace pale orange-brown, grey-brown on the head. Legs grey-brown and orange-brown. Chelicerae deep orange-brown. The abdomen is pale creamy-grey with dark brown spots forming a pattern of about five wide lines; there are also two parallel median lines in dark brown, running anterior to posterior. Ventral surface of the abdomen is pale yellow-brown with dense dark brown shading leaving only sparse patches of the base colour. The ventral surface of the prosoma is grey-brown.

Carapace

Fovea deep, dark and slightly procurved.

Eyes

The eyegroup occupies 27/79 of the width of the head. Viewed dorsally, the anterior row is slightly procurved and the posterior row is slightly recurved (almost straight). The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 4:3.

Sternum

Longer than wide in the ratio 49:45. The posterior pair of sigillae is larger than the median pair.

Palp

Tarsus and metatarsus with thick scopula. Claw with a strong basal tooth and a small tooh proximal to the midpoint.

Legs

Legs 1 and 2 with a thick scopula on the tarsi. Superior claws of leg 1 with a strong tooth proximal to the midpoint and another strong tooth at the midpoint.

Spinnerets

The lateral pair are longer than the medial pair in the ratio of 5:1.

Material examined

Holotype female. In a clay bank by Worsleys Road, S 43°34'48.1"E 172°36'37.8", Canterbury, December 2013, M. Provis, C. J. Vink, V. Smith (Canterbury Museum), beetled out of a lidded burrow.

Paratype female. 114 Dyers Pass Road . Under walnut tree in garden (S 43°34'43.3" E 172°37'49.2"), Canterbury, April 2014, P. Cochrane (Canterbury Museum), dug out of a burrow.

Etymology

This species is named after the Lawry family of Yaldhurst for their help, support, and friendship throughout this research project.

Species notes

This species is sympatric with *C. dendyi*, and the population beside Worsleys Road contains both species. The two species are morphologically and genetically different from *C. dendyi*. The holotype and paratype sequences differ by a large percentage (2.1%), and may be cryptic species. Morphologically they are not readily distinguishable, and the types were both found in close proximity to each other. Future research may split this species into two.

Figure 6.24: *Cantuaria lawryi* (female only). A) habitus dorsal B) habitus ventral C) genitalia D) first leg claw E) palp claw F) eye group.

Cantuaria mcquillani n.sp.

Fig. 6.25

Diagnosis

This species is most closely related to *C. prina* (see Forster 1968 for description) and *C. insidia*. The female's abdomen is pale with heavy patterning, and is much less hirsute than *C. insidia* which is also only very faintly patterned. The female genitalia is distinctive, resembling that of *C. magna* (see Forster 1968 for description) more than any of its closer relatives, but being less kinked than *C. magna*. The form of the tarsal claws is distinct, differing from the claw forms seen in *C. prina*, *C. insidia*, and *C. magna*. The male can be distinguished by its large size, very dark, heavily hirsute body, but with a visible pattern on the abdomen. The form of the male palp is distinctive and does not resemble that of *C. magna*. *Cantuaria mcquillani* is found on the Denniston plateau, and its range does not appear to overlap with any other described species.

Gene sequences

A CO1 sequence from this species was uploaded onto GenBank (see Appendix F). DNA sequences could only be obtained from one male and one female individual, but the CO1 sequences differed from sequences in their sister clade (*C. prina* and *C. insidia*) by 5.2–5.5%. The two *C. mcquillani* sequences differed from each other by 0.1%.

MALE

Measurements

Carapace length 10.7 mm	width 8.5 mm
Abdomen length 10.6 mm	width 7.1 mm

Colour

Carapace and legs dark purple-brown, almost black, with a red line running from posterior to the eyegroup midway towards the fovea. Chelicerae purple-black. The carapace is covered with fine golden hairs which give it a metallic sheen under the microscope. The abdomen is a pale creamy brown with dark, rectangular lateral patches, some of which are broken. The abdomen is covered with thick, black, bristle-like hairs. The ventral surface of the abdomen is beige with a few small dark patches and two dark quadrangles between the posterior book lungs. The ventral side of the prosoma is dark grey-brown with red sigillae. The median pair of sigillae are larger than the posterior pair.

Carapace

Fovea straight. Lateral margins with a row of black bristles.

Eyes

When viewed dorsally, the anterior row is procurved and the posterior row is slightly recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 18:13.

Sternum

Longer than wide in the ratio 13:9.

Palp

The triangular bulb tapers seamlessly to form the thin distal portion, which is curved and points ventrally at the end, towards the spinnerets. The tibia and tarsus are covered with long, stout hairs, but no spines are visible (they may be concealed by the hairs). Between two and three rows of short, stout spines line the edge of the tibial depression.

Legs

Scopula on the tarsus and metatarsus of leg 1. Superior claws on the first pair of legs with one weak tooth at the base and one strong trifid tooth proximal to the midpoint. Spurs leaf-like.

Spinnerets

The lateral pair are longer than the medial pair in the ratio of 35:11.

Material examined

Holotype male. Denniston, West Coast, S41°44'06.0" E171°46'54.0", February 2014, B. McQuillan (Canterbury Museum), found walking on forest floor at night.

Allotype female. Denniston, West Coast, June 2014, V. R. Smith (Canterbury Museum), beetled out of lidded burrow in clay bank beside walking track.

Etymology

This species is named after Bryce McQuillan, a spider enthusiast and photographer who found the holotype. The species is named in gratitude for the use of Bryce's excellent photographs to promote this research and gain funding.

Species notes

This species seems common in Denniston. The holotype male is larger than the allotype female.

FEMALE

Measurements

Carapace length 8.3 mm	width 6.3 mm
Abdomen length 10.4 mm	width 7.3 mm

Colour

Carapace tan-brown with some dark brown outlining the head and carapace. Legs yellow-brown. Chelicerae dark purple-black. The abdomen is pale cream with many small dark brown spots, some joined to form lines of various thickness. Ventral surface of the abdomen is beige and has a wide median dark triangle tapering towards the epigyne, and several scattered dark brown spots. Ventral surface of the prosoma is grey-brown. The entire ventral surface has a thin covering of brown setae.

Carapace

Fovea deep, dark and straight. Lateral margins with 1-2 rows of setae.

Eyes

When viewed dorsally, the anterior row is slightly procurved and the posterior row is slightly recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 7:5.

Sternum

Longer than wide in the ratio 7:6. The posterior and median pairs of sigillae are approximately the same size.

Palp

Tarsus and metatarsus with thick scopula. Claw with a strong basal tooth which is bifid on the proximal side. There are two small teeth proximal to the midpoint.

Legs

Leg 1 with a thick scopula on the tarsi and metatarsi. Leg 2 with thick scopula on the tarsi and distal two-thirds of the metatarsi. Superior claws of leg 1 with two strong teeth at the base, the distal tooth being larger than the proximal tooth. A small tooth is approximately at the midpoint along the claw.

Spinnerets

The lateral pair are longer than the medial pair in the ratio of 25:7.

Figure 6.25: *Cantuaria mcquillani*. Male: A) habitus dorsal B) habitus ventral C) first leg claw D) spurs E) palp F) abdomen. Female: A) habitus dorsal B) habitus ventral C) palp claw D) first leg claw E) spermatheca F) eye group.

Cantuaria olartei n.sp.

Fig. 6.26

Diagnosis

This species is most closely related to *C. vinki*. The colour of the carapace is much deeper and darker in *C. vinki*. *Cantuaria olartei* has a strong tooth at the base of its palp claw (*Cantuaria vinki* has a simple palp claw) and the first leg claws have two strong teeth. Other character differences are likely, but unable to be identified with confidence due to the poor preservation of the *C. vinki* type specimen. *Cantuaria olartei* is found in rural Blenheim, and its range may overlap with that of *C. vinki*, but the ranges of the two species distinguish them from the rest of the genus.

Gene sequences

Cytochrome oxidase subunit 1 sequences from *C. olartei* were uploaded onto GenBank (see Appendix F). *Cantuaria olartei* sequences differed from the sequence in their sister clade (*C. vinki*) by 5.5–5.7%.

FEMALE

Measurements

Carapace length 7.9 mm	width 6.1 mm
Abdomen length 11.2 mm	width 8.2 mm

Colour

Carapace and legs pale grey-brown with orange-brown patches. Chelicerae dark orange-brown. The abdomen is dark brown with thin light grey lines interspersed with light grey rounded patches. Two thick lines in light grey are at the anterior end of the abdomen, and there is a thin light grey median line. Ventral surface of the abdomen is pale creamy-grey with a broad dark brown median patch. The ventral surface of the prosoma is brown and covered with dark brown hairs.

Carapace

Fovea deep, dark and slightly procurved.

Eyes

The eyegroup occupies 2/5 of the width of the head. Viewed dorsally, the anterior row is slightly procurved and the posterior row is slightly recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 48:31.

Sternum

Longer than wide in the ratio 53:48. The posterior pair of sigillae is slightly wider than the median pair; sigillae are only faintly visible.

Palp

Tarsus with thick scopula. Claw with a strong basal tooth.

Legs

Legs 1 and 2 with a thick scopula on the tarsi. Leg 1 with a thick scopula on the metatarsi. Leg 2 with a thick scopula on the distal 2/3 of the metatarsi. Superior claws of leg 1 with a strong tooth near the base. A smaller strong tooth is located distal to the midpoint.

Spinnerets

The lateral pair are longer than the medial pair in the ratio of 7:2.

Material examined

Holotype female. Under walnut tree in garden near Blenheim, S 41°30'08.3" E 173°52'37.0", Marlborough, February 2014, V. Smith, J. Cooper, J. Stitchbury (Canterbury Museum), dug out of a lidded burrow.

Paratype of unknown gender (carapace only). Under walnut tree in garden near Blenheim (S 41°30'08.3" E 173°52'37.0"), Marlborough, February 2014, V. Smith, J. Cooper, J. Stitchbury (Canterbury Museum), dug out of a lidded burrow.

Etymology

This species is named after arachnologist Jagoba Malumbres-Olarte for his help, support, and friendship throughout this project.

Species notes

This species is plentiful in the garden where the types were found.

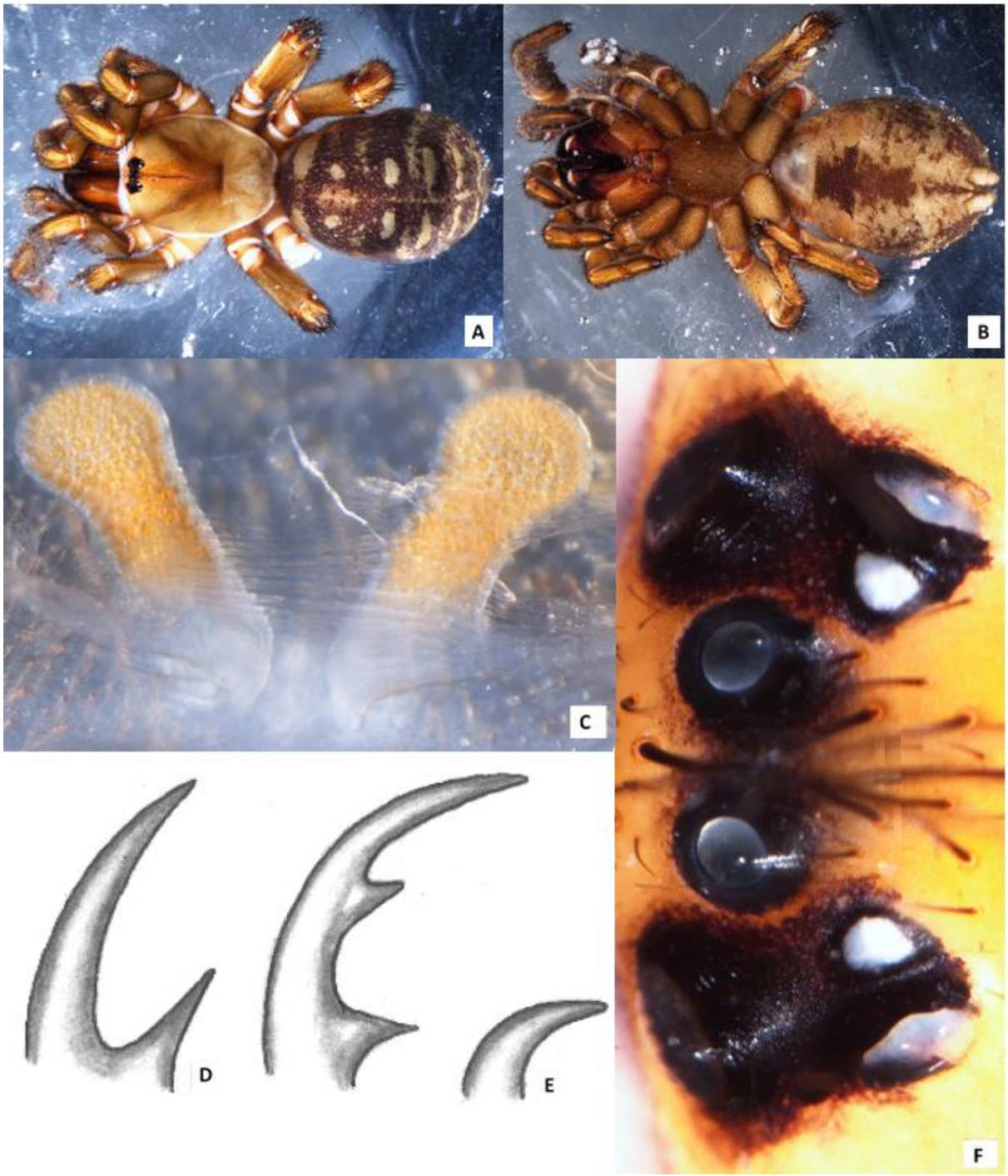

Figure 6.26: ***Cantuaria olartei*** **(female only). A) habitus dorsal B) habitus ventral C) genitalia D) palp claw E) first leg claw F) eye group.**

Cantuaria pollocki n.sp.

Fig. 6.27

Diagnosis

This species is most closely related to *C. vellosa*, *C. napua* (see Forster 1968 for descriptions) and females found in Kakanui that may be *C. kakanuiensis*. The most distinctive character is the claw form, which does not resemble that of any of its closest relatives. *Cantuaria pollocki* is smaller than *C. vellosa*, not so hirsute, and has different markings on the abdomen forming broken stripes rather than a folium. The markings are bolder on *C. pollocki* than on *C. napua*, and the form of the spermathecae is very different: they point straight at a 45 degree angle rather than bending to the side. The female *C. kakanuiensis* has yet to be described, but females found in Kakanui from a distinct species are larger than *C. pollocki*. Their abdomen colouration and genitalia form is unknown so cannot be compared, but the two species are unlikely to inhabit the same area. This species was found while searching for *C. marplesi* (Todd, 1945), but the claw form, abdomen colouration and spermathecae do not at all resemble Forster's (1968) description. *Cantuaria pollocki* and *C. marplesi* are both found in Duntroon, and their range may overlap with that of *C. vellosa,* but distinguishes them from most other species in the genus.

Gene sequences

Cytochrome oxidase subunit 1 sequences from this species were uploaded onto GenBank (see Appendix F). Genetic variation between the two specimens tested was 3.9%. *Cantuaria pollocki* sequences differed from the sequence in their sister clades by 3.4–4.7%. They were most closely related to sequences from female *Cantuaria* found in Kakanui.

FEMALE

Measurements

Carapace length 10.9 mm width 4.2 mm

Abdomen length 10.8 mm width 7.9 mm

Colour

Carapace and legs pale yellow-gold, with dark brown patches on the legs and carapace behind the head. Chelicerae dark brown. The abdomen is pale creamy gold with indistinct brown patterning, shaded heavily towards the anterior but less towards the posterior. Ventral surface of the abdomen is light brown with two dark brown median patches. Ventral surface of the

prosoma is grey-brown with dark brown patches. The entire ventral surface is covered with long dark brown hairs.

Carapace

Fovea dark and slightly procurved.

Eyes

The eyegroup occupies 37/137 of the width of the head. Viewed dorsally, the anterior row is slightly procurved and the posterior row is slightly recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 11:7.

Sternum

Longer than wide in the ratio 17:12. The posterior two pairs of sigillae are only faintly visible.

Palp

Tarsus with thick scopula. Claw with a strong bifid tooth at the base.

Legs

Legs 1 and 2 with a thick scopula on the tarsi and metatarsi. Superior claws of leg 1 with a strong tooth near the base and a wide semicircular pentafid tooth resembling a buzz saw proximal to the mid-point.

Material examined

Holotype female. In clay under plum tree in the Duntroon School playground. S 44°51'20.8" E 170°41'07.5". Central Otago, March 2014, V. Smith (Otago Museum), beetled out of a lidded burrow.

Paratype female. In clay under plum tree in the Duntroon School playground. (S 44°51'20.8" E 170°41'07.5"). Central Otago, March 2014, V. Smith (Otago Museum), beetled out of a lidded burrow.

Etymology

This species is named after Burns Pollock of the Vanished World Museum in Duntroon, in gratitude for his help in finding specimens, and his kindness and enthusiasm for this research.

Species notes

The holotype and paratype of this species were recovered as different species by the PTP analysis, and future research may find that they are different species. They differ more genetically from each other than they do from morphologically dissimilar females found in Kakanui. However, the paratype only consists of a prosoma, and there are no character differences between it and the holotype. The two individuals were also both found in the same location (Duntroon). Therefore, in this thesis they are considered the same species.

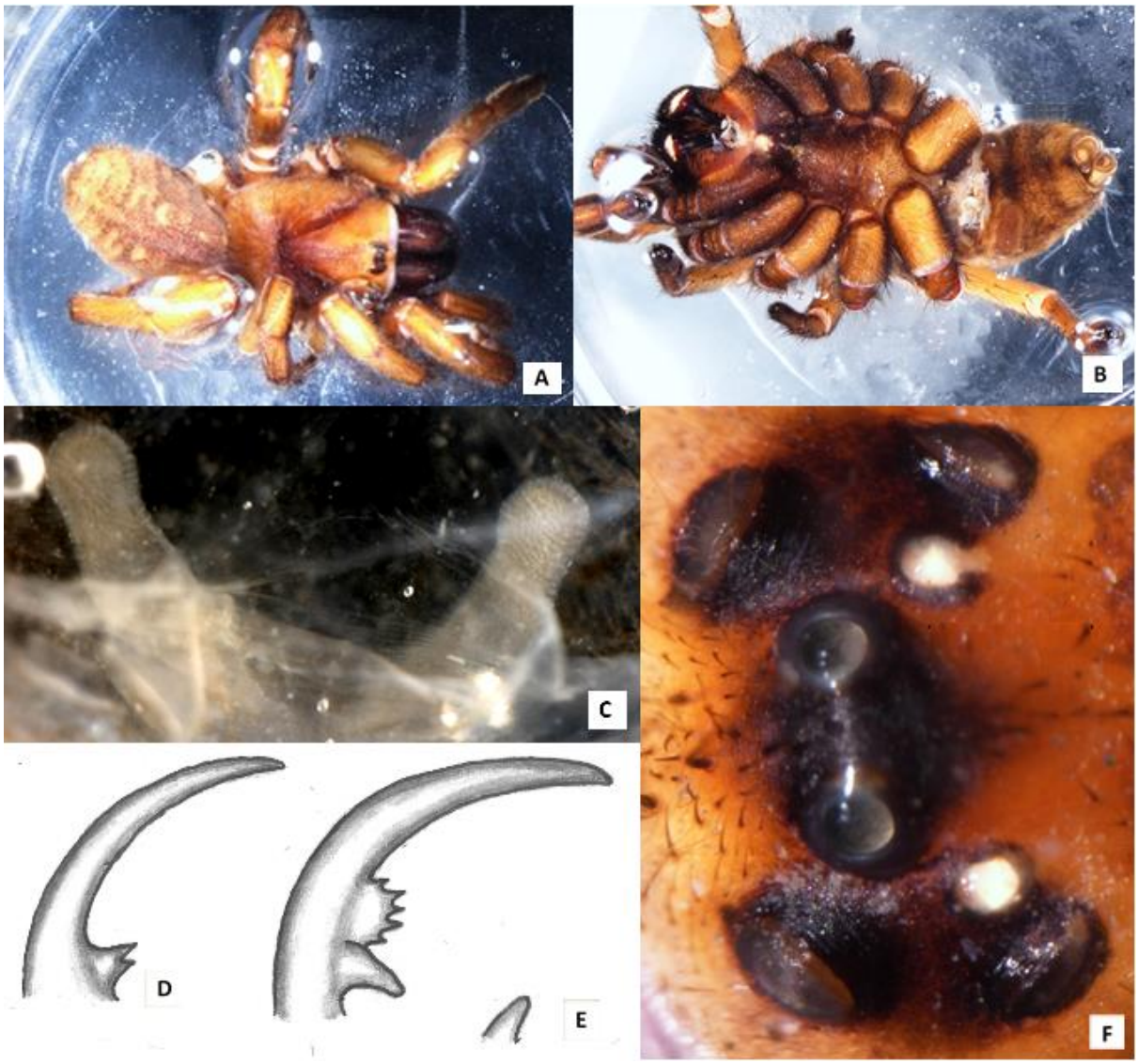

Figure 6.27: *Cantuaria pollocki* (female only). A) habitus dorsal B) habitus ventral C) genitalia D) first leg claw E) palp claw F) eye group.

Cantuaria vinki n.sp.

Fig. 6.28

Diagnosis

This species is most closely related to *C. olartei*. The colour of the carapace is much deeper and darker in *C. vinki*. *Cantuaria vinki* has a simple palp claw (*C. olartei* has a strong tooth at the base of its palp claw) and the first leg claws have a single small tooth in addition to the strong basal tooth (*C. olartei* has two strong teeth on its first leg claws). Other character differences are likely, but unable to identify with confidence due to the poor preservation of the type specimen. *Cantuaria vinki* is found in suburban Blenheim. Its range distinguishes it from most other species of *Cantuaria*, but may overlap with that of *C. olartei*.

Gene sequences

A CO1 sequence from this species was uploaded onto GenBank (see Appendix F). DNA sequences could only be obtained from one individual, but the CO1 sequence differed from sequences in its sister clade (*C. olartei*) by 5.3–5.7%.

FEMALE

Measurements

Carapace length 11.4 mm width 8.0 mm

Abdomen unknown

Colour

Carapace dark orange-brown. Legs orange-brown. Chelicerae dark brown. The ventral surface of the prosoma is brown and covered with many dark brown hairs.

Carapace

Fovea deep and straight.

Eyes

The eyegroup occupies 27/65 of the width of the head. Viewed dorsally, the anterior row is slightly procurved and the posterior row is slightly recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 55:38.

Sternum

The sternum is longer than it is wide in the ratio of 8:7.

Palp

Tarsus with thick scopula. Claw simple and curved.

Legs

Legs 1 and 2 with a thick scopula on the tarsi. Leg 1 with a thick scopula on the metatarsi. Leg 2 with a weak scopula on the distal portion of the metatarsi. Superior claws of leg 1 with a small basal tooth and another small tooth proximal to the midpoint.

Spinnerets

Unknown.

Material examined

Holotype female. Found outside 10 Kingwell Drive in Blenheim, S 41°30'19.7" E 173°56'19.7". November 2014, S. Lyon (Canterbury Museum). Originally preserved in methylated spirits, so that the abdomen and parts of the legs are degraded and discoloured.

Etymology

The species is named after Cor Vink, in gratitude for his help in producing this thesis and introducing me to arachnology in general and *Cantuaria* in particular.

Species notes

This species is known only from a single female specimen which is in poor condition, so that a complete description cannot be made. Further collection and sequencing is required so that more morphological characters can be identified for the benefit of researchers who do not have access to a molecular laboratory.

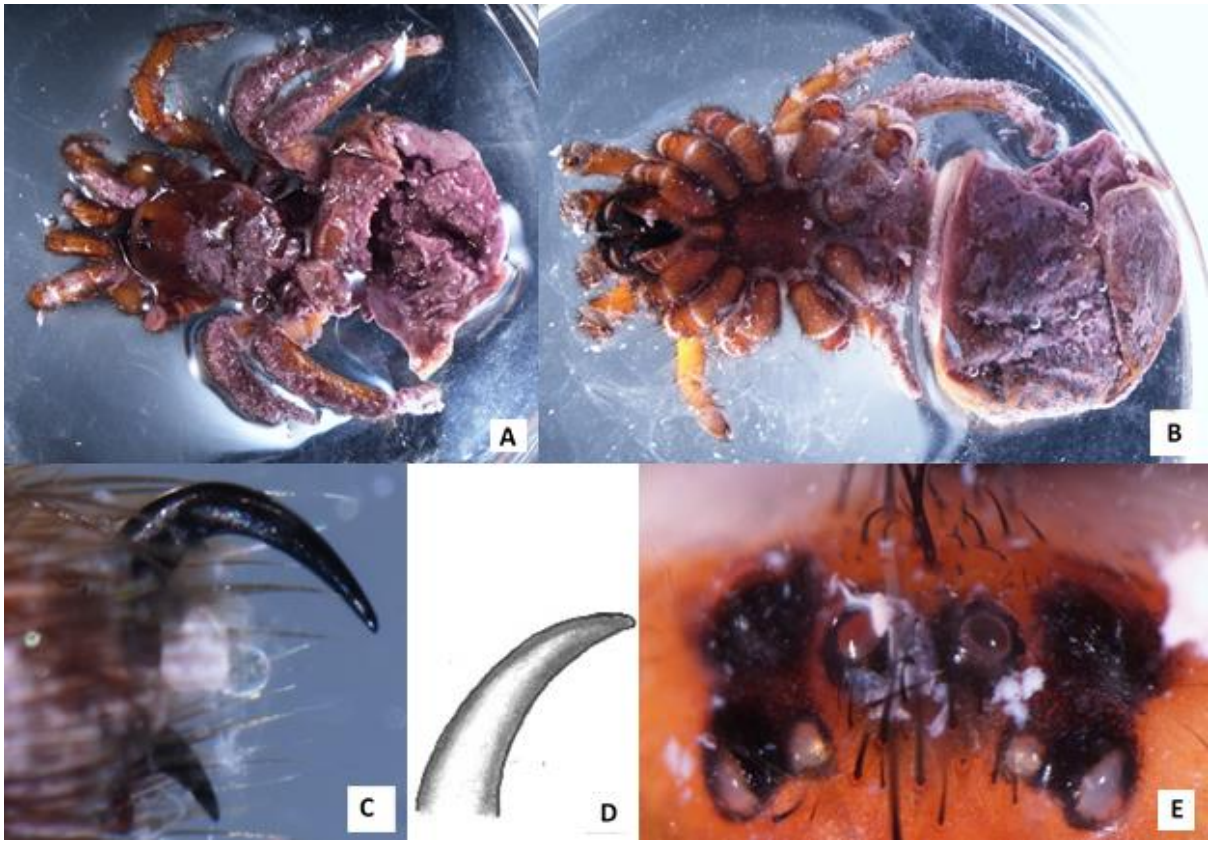

Figure 6.28: *Cantuaria vinki* (female only). A) habitus dorsal B) habitus ventral C) first leg claw D) palp claw E) eye group.

Cantuaria viridaria n.sp.

Fig. 6.29

Diagnosis

The dorsal surface of the abdomen resembles that of *C. myersi* (see Forster 1968 for description), its closest relative. The claw form differs from that of *C. myersi*: the palpal claw has a bifid basal tooth rather than a medial tooth. This species is found in Days Bay, Wellington.

Gene sequences

A CO1 sequence from this species was uploaded onto GenBank (see Appendix F). DNA sequences could only be obtained from one individual, but the CO1 sequence differed from its sister species (*C. myersi*) by 5.8–5.9%. The two *C. myersi* specimens differed from each other by 0.2%.

FEMALE

Measurements

Carapace length 10 mm	width 8 mm
Abdomen length 9.5 mm	width 8.5 mm

Colour

Carapace grey-brown, legs brown and orange. Chelicerae dark brown. The abdomen is pale creamy brown, with variable dark brown patterning in the form of patches and broken lines. Ventral surface of the abdomen is pale brown with dark brown median triangular patches. Ventral surface of the prosoma is dark grey-brown with dense black hairs.

Carapace

Fovea dark and slightly procurved.

Eyes

The eyegroup occupies 22/67 of the width of the head. Viewed dorsally, the anterior row is procurved and the posterior row is recurved. The median ocular quadrangle is wider posteriorly than anteriorly in the ratio of 31:21.

Sternum

The sternum is longer than wide in the ratio of 14:11.

Palp

Tarsus and metatarsus with thick scopula. Claw with a strong basal tooth which has a small tooth on its proximal edge.

Legs

Legs 1 and 2 with a thick scopula on the tarsi and metatarsi. Superior claws of leg 1 with a strong tooth at the base which is bifid proximally.

Spinnerets

The lateral pair are longer than the medial pair in the ratio of 16:3.

Material examined

Holotype female. Williams Park, Days Bay, Wellington S 41°16'48.1"S E 174°54'26.4". May 2014, V. Smith (Museum of New Zealand), caught by beetling from lidded burrow in clay bank beside path.

Paratypes female (four individuals). Williams Park, Days Bay, Wellington S 41°16'48.1"S E 174°54'26.4". May 2014, V. Smith (Otago Museum), caught by beetling from lidded burrow in clay bank beside path.

Etymology

The species name is derived from the Latin word *viridarium* – plantation garden, as all specimens of this species were found in Williams Park, a large and elaborate garden with many trees.

Species notes

This is the third species of *Cantuaria* to have been found in the North Island. It is plentiful in Williams Park. The specimens found at Days Bay that were identified by Forster as *C. myersi* are possibly also *C. viridaria*.

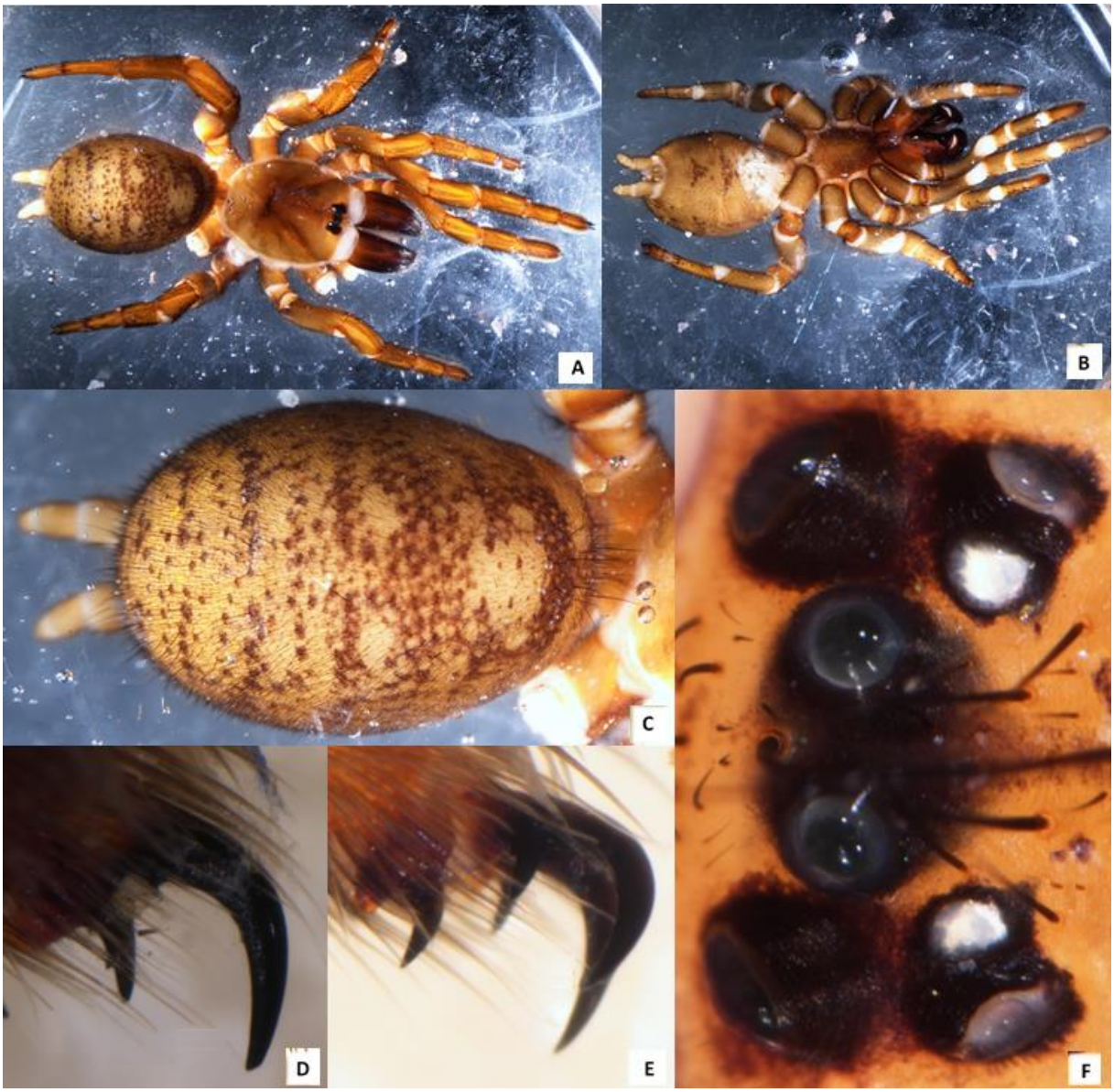

Figure 6.29: *Cantuaria viridaria* (female only). A) habitus dorsal B) habitus ventral C) abdomen dorsal D) palp claw E) first leg claw F) eye group. E and F are images of another individual from the same population that morphologically and genetically resembled the type.

6.4 Discussion

The aim of this chapter was to explore the taxonomy of the genus *Cantuaria*, focusing on describing new species as they are found. Using molecular phylogenetics, I revealed the structure and evolutionary relationships within the genus, including 12 new species.

Forster's (1968) descriptions and species designations were largely correlated with phylogenetic species designations using the PTP, but *C. johnsi*, *C. dendyi*, *C. marplesi*, and *C. wanganuiensis* were all found to consist of more than one species. Forster's clades (Table 6.1) were difficult to compare to the phylogenies due to incomplete sampling, but the clades supposed by Forster were largely consistent with those in the phylogeny. Forster based his descriptions entirely on morphology, which does not always correlate with the genetically derived phylogeny in this genus. Specimens identified by Forster and held at Otago Museum were often undissected, and showed variation from the species description, indicating that Forster believed geographical location and general appearance to be as important, if not more important, than character morphology. My results provide evidence that individual character morphology does not always vary more between species than within species, but overall morphology, geographical location, and molecular characters are the most important tools for determining species.

The morphology-based clades suggested by Forster (1968), and shown in Table 6.2, are somewhat supported by phylogenetics. Relationships vary between phylogenies, however, and do not appear to represent consistent clades that support Forster's classification. Deciding whether or not some of Forster's (1968) species are present in the phylogeny is difficult, but given the geographical restrictions and local endemicity shown by this species, it is likely that specimens found in the type location of a particular species are individuals of that species. However, some species (e.g. within the *C. dendyi* complex) have large ranges that overlap with the ranges of other species. Anthropogenic processes, such as quarrying, may also change the range and distribution of some species, as earth and burrows may be moved together from one location to another. Therefore, geographic location cannot always be used as a reliable diagnostic tool.

This project found that morphological characters are of limited use in the taxonomy of *Cantuaria*. I focused on the characters that have been previously used to identify idiopids in general and *Cantuaria,* in particular; mainly genitalia. However, tarsal claws, abdomen colouration, and leg spination are of limited use. Eye pattern was not scrutinised heavily in this research, and may be found to be a useful character. However, I doubt the utility of eye pattern in species diagnostics, due to its lack of variability and susceptibility to teratogeny. Researchers without access to molecular facilities may find combinations of characters useful when combined with geographic location, but species designations based only on morphological characters may be inaccurate.

The genus *Cantuaria* was previously recognised as containing 42 species: 2 in the North Island, and 40 in the South Island. Included in the South Island species were 13 species of a morphologically distinct ecotype that builds unlidded burrows. My study provides evidence for 12 new species in the lidded burrow ecotype. Some of the species in the unlidded ecotype may in future be synonymised, as they are morphologically and genetically very similar (e.g. *C. delli;* Forster, 1968*, C. stewarti;* Todd, 1945 and *C. isolata;* Forster, 1968). However, I was unable to obtain CO1 sequences for specimens from these locations, so they were excluded from my PTP species delimitation. The currently recognised genus *Cantuaria* also appears to consist of two separate genera; genetic evidence suggests that the two ecotypes (the unlidded "*huttoni*" ecotype and the lidded "non-*huttoni*" ecotype; Forster & Wilton, 1968) diverged 16 million years ago (see Chapter 5). Species within the unlidded ecotype have dome-shaped female genitalia (Fig. 6.1), and males have a short, stout bulb. In contrast, the lidded ecotype of *Cantuaria* (containing the type species *C. dendyi*) has more elongate, club-shaped female genitalia and males have a longer bulb. Palpal and first leg tarsal scopulae are thick and dense in the lidded ecotype, while the unlidded ecotype has thin, weak scopulae. Additionally, Multi-locus phylogenies recover the unlidded ecotype as a well-supported sister taxon to the rest of *Cantuaria* (Chapter 5). However, the low posterior probabilities in key areas of the single locus trees, combined with variable placement of *C. insulana*, prohibit firm conclusions from being made regarding the molecular status of the two genera. Due to their morphological and ecological similarities, it is likely that the 13 species within the *huttoni* ecotype would resolve within the same genus, but difficulty in obtaining sequence data prohibits a definitive species list from being made here. Thus, they are not described here, and future research is required to resolve the possibility of two genera.

The distinction between unlidded and lidded ecotypes is not useful for diagnosis, as preliminary data suggest that the lid-building behaviour is a reaction to environmental conditions, and an individual may build a lidless burrow in damp forest but a lidded burrow in dry conditions (V. Smith, unpublished data). Further, Forster (1968) noted that *C. wanganuiensis* and *C. parrotti* both build lidless burrows, but are included in the lidded clade.

My sampling of the genus *Cantuaria* is incomplete, but assuming that previously described species that were not sampled are correct, there appear to be two New Zealand genera in the family Idiopidae. The larger genus, *Cantuaria*, contains 41 species, while the smaller unnamed genus contains 13 species, some of which may be synonymised in the future. The unnamed genus is not described here due to the need for more sampling within that genus, and further analysis to confirm monophyly.

My research forms part of a growing body of evidence suggesting that some arachnid taxa, such as harvestmen (Opiliones) (Emata & Hedin 2016) and mygalomorphs (Bond et al. 2012; Hamilton et al. 2011; Starrett & Hedin 2007), have morphology that does not always follow molecular relationships. Mygalomorphs in general have highly conserved morphology (Bond et

al. 2001; Hendrixson & Bond 2007; Starrett & Hedin 2007). One mygalomorph genus, *Aliatypus*, contains at least three cryptic species, which have been described in a similar way to the species descriptions presented in this chapter: the general morphology and geographic location are given, but emphasis is placed on diagnosis using gene sequences (Satler, Carstens & Hedin 2013).

Sampling for this study did not include all type locations (e.g. Stephens Island), and populations could not be found in some type locations, despite thorough searching (e.g. Makarora). Further, type specimens for previously described species could not be sequenced. However, I believe that the phylogenies constructed for this study are comprehensive and largely representative of the evolutionary relationships between New Zealand Idiopidae. Future studies may use more advanced molecular techniques to obtain DNA from a greater number of samples, and some species from the unlidded idiopids may be synonymised. Future sampling should include collecting both males and females from populations, as many *Cantuaria* species are only described from one sex. For example, *C. kakahuensis* females are not described. Females were found in Kakahu, and are likely to be *C. kakahuensis*; however, males from the same population were not found, and investigating the possibility of more than one species in the Kakahu area was beyond the logistical scope of this study. Therefore, female *C. kakahuensis* are not described here, but future taxonomic work should aim to clarify the species status of *Cantuaria* in Kakahu. The new species described in this chapter are unlikely to be undescribed sexes for existing species; most are from new locations. Specimens found where previously described species have been found were examined for morphological similarities to those species, unless they were a different sex to the one described, in which case they were considered likely to be that species and were not described as new species. More species are also likely to be found in the future, as the current study focused on collecting as many species as possible from more accessible areas. Central Otago, the West Coast, and Nelson areas may have more populations in native habitat that is far from roads. Additionally, some populations were found but not sampled due to time constraints. Trapdoors were found in Burkes Pass Scenic Reserve beside the road (approximately -44°05'28.1", 170°35'07.2"), Rangiora High School around the bases of trees (S 43°17'51.9", E 172°35'52.4") and at Punakaiki (S 42°05'32.7", E 171°20'40.3").

Despite the large degree of geographically localised endemism shown by the genus *Cantuaria*, some species have large ranges. For example, *C. fountainae* was found in Lincoln, Christchurch and Eyrewell, within an area encompassing at least 250km^2. Other species appear to have small ranges, although the full range of those species may be larger than can be easily ascertained. For example, *C. napua* was only found in one patch of grass (about 200 m^2) beside a road, despite searching the surrounding area, although the species may be present on private property. To some extent, vicariance may drive speciation in *Cantuaria*: species are highly divergent on either side of the Southern Alps, and the braided rivers of the Canterbury Plains may partially explain the high number of species there. Two of the North Island species (from

Wellington and Whanganui) are more closely related to specimens from Blenheim than they are to a third North Island species (from Wellington). Their close relatedness may be due to dispersal, or due to the former land connection between the North Island and the South Island (Trewick & Bland 2011). There may be some recent dispersal across water: ITS and H3 sequences suggest that *C. stewarti*, *C. delli*, and *C. isolata* are very closely related to *C. sylvatica*, despite all four species living on separate landmasses and being separated by hundreds of kilometres. Alternatively, the four species may have shared a large, continous expanse of habitat which has subsequently become fragmented.

Most of the specimens sequenced were from large populations that did not appear to be threatened, except for possible habitat fragmentation. However, *C. insidia* was found in a highly developed area, and only one individual was found despite thorough searching. When soil is uplifted and moved elsewhere, or heavily disturbed, burrows are destroyed and individuals can be injured or killed. *Cantuaria* spp. take years to reach sexual maturity, lay few eggs per year, and invest heavily in parental care (Irish 2001, see also Chapter 8). The dense populations formed by *Cantuaria* burrows often cover only small areas, so that a single landscaping event could destroy many burrows and cause a previously thriving population to decline and become threatened. There are likely to be more species of *Cantuaria* yet to be described, some of which may be in urban areas and also under threat. Others may be deep in the bush, threatened by land clearance or mining. *Cantuaria* is a highly speciose genus, and it is possible that some species may only consist of one population due to the general lack of dispersal ability shown by *Cantuaria* spp. and range contraction due to human land use.

The current study represents the first taxonomic treatment of the genus *Cantuaria* since 1968. Previous taxonomy agreed largely with phylogeny, perhaps partially due to the intelligent interpretation of geographic location, but morphological characters that were used are not always more consistent within species than between species. The current study has added 12 more species to the genus *Cantuaria*, but also provides evidence that the genus should be split into two genera. *Cantuaria* continues to be the third most speciose genus of the family Idiopidae (World Spider Catalogue 2016). The taxonomy results presented in this chapter have implications for biogeography and conservation, and further adds to current understanding of the highly diverse spider fauna of New Zealand.

Chapter 7
Habitat requirements of the genus *Cantuaria*

7.1 Introduction

Habitat requirements are the set of conditions necessary for a taxon to survive and reproduce in a particular environment (Smart et al. 2006; Tellería 2016). A taxon's habitat requirements form a fundamental aspect of its niche and subsequently affect their distribution (Panzacchi et al. 2015; Whittaker, Levin & Root 1973). The parameters included in a particular taxon's habitat requirements can be many and complex, and include both biotic and abiotic factors. Depending on a particular species' life history strategy, its habitat requirements will most likely involve the parts of the environment with which it frequently interacts. For example, spiders that live on the surface of the ground may build their webs in vegetation, or otherwise navigate it. They also depend upon insects living in the vegetation. Therefore, vegetation type can be an important biotic factor for spider habitat, and particular spider taxa may require particular vegetation types as part of their habitat requirements (Griffiths 2001; Malumbres-Olarte et al. 2013; Smith et al. 2014). Some spiders, such as lycosids, theraphosids and idiopids, may live part or all of their lives in underground burrows; soil parameters such as particular moisture levels may form part of their habitat requirements (Engelbrecht 2013; M'rabet et al. 2007).

An organism's dispersal ability is influenced by the environmental parameters that it is capable of withstanding (Broady & Smith 1994; de Vries, den Boer & van Dijk 1996; Dickman & Doncaster 1989). Organisms that have a very narrow range of habitat requirements may be less able to disperse long distances than more adaptable organisms. During dispersal, an organism may pass through different habitat types, different climates, or even different biomes. Even if the environmental conditions in the final destination are conducive to the survival of the organism, conditions along the journey may be so inhospitable that the traveller may not survive. For example, three genera of Cyphophthalmi (mite harvestmen) that are endemic to New Zealand can only survive within very narrow environmental parameters (particularly vegetation type, moisture and rainfall; Boyer & Giribet 2009). The mite harvestmens' lack of adaptability to different habitat types may be a major contributor to their lack of dispersal ability. Boyer and Giribet (2009) noted that species within the suborder Cyphophthalmi were restricted in range by their habitat, leading to localised endemism in areas with discontinuous habitat. Mite harvestmen and other arachnids, such as spiders, have colonised a diverse array of habitats and ecological niches on every continent. Their life histories vary from generalist to highly specialised. No example has yet been found of a spider lineage with strict habitat requirements that appears to be a remnant of the breakup between Zealandia and Gondwana. Other New Zealand fauna, such as Lycosidae (wolf spiders; Vink & Paterson 2003), *Zosterops* (silvereye; Estoup & Clegg 2003), and galaxiid fish (Burridge et al. 2012; Waters et al. 2000), are

able to adapt to a wide variety of habitat types, and have managed to survive dispersal to New Zealand over the Tasman Sea.

A taxon's ability to disperse and colonise large geographic areas is influenced by many factors, and habitat preferences may change over long periods of time through evolution. However, the inability to quickly adapt to a range of environmental conditions may limit a taxon's recent native geographic range. Understanding a taxon's range of habitat requirements may provide insight into its ability to disperse, and therefore its recent biogeographic history. Over evolutionary time, however, dispersal and colonisation ability may become less predictive of distribution, as random events, such as rafting, may transport even dispersal-limited species between areas that are able to support populations. Additionally, a narrow range of suitable habitat types may not limit dispersal ability if it includes parameters that allow it to survive an oceanic journey. For example, the spray zone spider, *Amaurobioides* sp., only inhabits coastal rock crevices, but has nonetheless undertaken multiple oceanic colonisations between Australia, Tasmania and New Zealand (Opell, Helweg & Kiser 2016). Likewise, New Zealand's endemic widow spider, *Latrodectus katipo*, demonstrated an ability to survive prolonged salt water exposure in experiments (Griffiths 2001). The range of *L. katipo* includes most of New Zealand's coastline, and molecular evidence suggests it survived dispersal from Australia over the Tasman Sea (Griffiths, Paterson & Vink 2005).

Researching habitat requirements can provide information used to predict taxon distributions in both time and space (Fouquetet al. 2010; Peterson, Ball & Cohoon 2002; Wasserman et al. 2012), identify areas where important habitat types are at risk (Bell, Wheater & Cullen 2001; Smart et al. 2006), and illuminate hitherto unknown aspects of organism ecology (Fouquet et al. 2010). Other benefits gained by identifying habitat constraints include recognition of which areas of habitat are required by an organism to survive and reproduce. For example, Smith et al. (2014) tracked the seasonal population dynamics of the widow spider *L. katipo* in native and introduced vegetation. Introduced grass was found to be used much less by *L. katipo* as a habitat than native sedge, emphasising the importance of native sedge habitat conservation to *L. katipo.*

Many habitat parameters are affected by climate; for example, annual rainfall contributes towards soil moisture, and future weather patterns may alter the biomass and species composition of forests (Overpeck, Rind & Goldberg 1990). Habitat destruction and fragmentation is a major threat to biodiversity both globally (Pimm et al. 2014) and within New Zealand (Brooks et al. 2002; Ewers et al. 2006). As increasing areas of native New Zealand habitat are lost to exploitation (Norton & Miller 2000), such as by agriculture (Baskaran, Cullen & Colombo 2009; Fountain, Wratten & Dymond 2013; Myers et al. 2013), investigating which areas require most protection from disturbance and destruction is paramount to conserving New Zealand's native wildlife.

While previous habitat conservation decisions were based on subjective suppositions, modern inference uses tools of statistical analysis (for example, ecological niche modelling), and mapping, such as geographic information systems (GIS). These more rigorous methods can more accurately define the limits of a species' range, and infer which areas are most suitable for the species based on what types of habitat support numerous individuals (Denoël & Ficetola 2015). Ecological niche modelling is a particularly useful tool, employing computer algorithms to predict the parameters that describe a species' niche based on their known distribution. For example, Denoël and Ficetola (2015) collected abundance data for paedomorphs of the endangered palmate newt (*Lissotriton helveticus*) in 277 ponds within 442 km^2 of rural France. Ecological niche modelling was combined with kernel density estimators (KDE, a method of predicting an animal's home range), to delineate specific areas that must be conserved for *L. helveticus* to survive.

A variety of different approaches to modelling habitat requirements exists, usually involving collecting data on both the known distribution of the focal taxa, and the habitat parameters that may affect their survival and reproduction (Brotons et al. 2004; Tsoar et al. 2007). The data can then be interpreted by modelling, and used to predict what factors may contribute to the habitat requirements of the organism.

Identifying an organism's habitat requirements allows the prediction of what could happen in the future, for example, under different scenarios of climate and habitat change. Habitats consist of different interlinked abiotic and biotic factors, many of which are affected by climate. For example, the genetic structures of alpine plant populations are affected heavily by an increase in global temperature (Jay et al. 2012). Plants form a vital part of the habitat for alpine animals. Vegetation and snow packs in the Rocky Mountains are expected to occupy higher ground in the warmer conditions predicted for climate change. As a result, American pine martens (*Martes americana*) are likely to suffer population fragmentation (Wasserman et al. 2012). The effect of climate change on Australian arthropod communities was inferred in a study examining community dynamics along a latitudinal gradient (Andrew & Hughes 2005). The study concluded that climate change would not affect the group structure of arthropod communities on host plants, but that species composition would change as a result of rising temperatures.

Niche modelling has been used to investigate habitat requirements of many different taxa. The trapdoor spider family, Idiopidae, would also benefit from niche modelling. Worldwide, idiopid ecology has been the subject of few research studies; their burrows are very cryptic and difficult to locate, and the spiders are hard to extract from their burrows (Engelbrecht 2013; Gupta 2011; Smith et al. 2015). *Idiops* sp. (possibly *I. joida;* Gupta, Das & Siliwal 2015), from the Western Ghats of India, was found to prefer open habitat with a small (10–30%) amount of vegetation cover. The roots of plants were thought to obstruct burrow construction when vegetation was dense (Gupta 2011). A separate study in the same area found that *I. joida* prefers

steep slopes and open habitat, with no vegetation present, or only sparse cover. *Idiops joida* appears to prefer drier soil in which to burrow, and burrows become more clustered in disturbed habitats (Gupta et al. 2015). A South African study used pitfall trapping to determine that males of different idiopid species are active at different times of the year, and that they are most active under conditions of high rainfall and soil moisture (Engelbrecht 2013); however, this study only focused on males searching for females.

Most knowledge concerning idiopid ecology is from unpublished studies and anecdotes. The New Zealand genus *Cantuaria* (see Chapter 2 General Introduction for a description) is not well-studied. Some aspects of general ecology (Marples & Marples 1972; Todd 1945) and the relationship between *Cantuaria* and a parasitic nematode (Poinar Jr & Early 1990), are known. The ecology and conservation issues of *Cantuaria* spp. are also discussed in a book, although the evidence presented is largely anecdotal and unpublished in scientific journals (Irish 2001). Todd (1945) described *Cantuaria* spp. (previously referred to as *Arbanitis*) as always living in a burrow with a trapdoor lid. *Cantuaria huttoni* was noted as an exception, as it does not build a lid. This lidless observation probably referred to the 13 species that Forster (1968) grouped into the *huttoni* group of species. *Cantuaria's* strictly local distribution was described, as was the fact that only males leave the burrows, based on evidence from little owl (*Athene noctua*) gut contents. Todd's (1945) observations form a reliable introduction to my knowledge of *Cantuaria* ecology, but are not comprehensive enough to build a basic picture of their life history. The only other major paper concerning *Cantuaria* spp. was a highly descriptive account of *Cantuaria* ecology (Marples & Marples 1972).

Marples and Marples (1972) aimed to form the basis for future *Cantuaria* ecology research. Juvenile *Cantuaria* are described as building their own burrows close to their mother's burrow, without actively dispersing; they were observed in burrows throughout the year, and offspring of different sizes were found in the burrow with their mother. New, smaller burrows appeared next to maternal burrows, indicating that offspring had left and built new burrows. Marples and Marples (1972) studied the Otago *Cantuaria* populations (focusing on *C. toddi*). Suitable habitat types identified included the base of slopes, with sparse vegetation and few rocks. However, Marples and Marples (1972) also noted that *Cantuaria* spp. could be found in moist, rocky habitats covered with vegetation. Additionally, they observed that *Cantuaria* spp. have a patchy distribution, with some areas (for example around Arrowtown and Queenstown) devoid of populations despite plenty of available habitat. However, *Cantuaria* may have been present in these areas but not found by Marples and Marples (1972), as the burrows are difficult to locate, particularly during dry weather and where dense vegetation covers the ground.

This chapter builds upon the research outlined above, with the overall aim of determining the major parameters affecting *Cantuaria* habitat requirements. Previous research has identified that soil moisture (Gotelli 1993; M'rabet et al. 2007; Rushton & Eyre 1992) and pH (van Straalen 1998) affect population abundance of mygalomorph spiders and other terrestrial and fossorial

arthropods. For example, ant lions were found not to burrow in soil that had recently been rained upon, possibly due to the crust formed on top of the soil as a result of rainfall; they were only found where the soil had a low moisture content (Gotelli 1993). Van Straalen (1998) found that different arthropod taxa preferred different soil pH, and the pH of the soil could be determined by examining the arthropod communities it supported. Based on this previous research, I hypothesise that *Cantuaria* spp. are sensitive to soil parameters such as moisture and pH. There may also be other habitat requirements important for *Cantuaria*, such as vegetation type (Malumbres-Olarte et al. 2013). Alternatively, *Cantuaria* may tolerate a wide range of habitat types, and have relatively non-specific habitat requirements.

Anthropogenic activity, such as vehicular traffic, farming, and pedestrian traffic, may also affect *Cantuaria* populations. Arthropod communities can be affected by human disturbance. Brazilian arthropod communities, for example, were shown to be highly affected by small-scale disturbance, such as logging and hunting (Uehara-Prado et al. 2009), with some arthropod taxa present in lower numbers in disturbed areas, while others were absent in disturbed areas but abundant in undisturbed areas. The major human disturbance types experienced by *Cantuaria* populations in New Zealand would most likely include farming and agriculture, pedestrian and vehicular traffic. I aim to test whether any of these disturbance types affect *Cantuaria* presence or absence.

In this study, I model data concerning soil and vegetation parameters that may be of importance to the future survival of New Zealand's endemic Idiopidae, under current predictions of climate change and habitat destruction. The results presented in this chapter may indicate particular threats to *Cantuaria* populations from human activity or climate change.

In this chapter, I investigate the habitat requirements (particularly soil, climate and vegetation parameters) of the New Zealand trapdoor spider genus *Cantuaria*. The paucity in published research of *Cantuaria* habitat requirements necessitates their study, as the results will have implications both for New Zealand biogeography research (Boyer & Giribet 2009; Crisp et al. 2011), and for conservation ecology.

7.1.1 Research aim and objectives/ research questions

The aim of this chapter is to investigate *Cantuaria* habitat requirements through ecological niche modelling. Using spatial mapping and field data to model *Cantuaria* habitat requirements, I will be able to uncover what environmental parameters affect their distribution in the past, present and future. This chapter will address the following research questions:

1. How great is the range of environmental conditions that is able to support the survival and reproduction of *Cantuaria* populations?

2. What environmental parameters (including soil, vegetation and climate-related parameters) affect the distribution of *Cantuaria* populations?

3. To what extent are *Cantuaria* population distributions affected by direct anthropogenic disturbance?

7.2 Methods

Two datasets were collected and analysed separately to model *Cantuaria* habitat requirements. Data collected for this study at specific population locations is referred to as the 'fine-scale dataset'. Locations of populations in diverse habitats throughout New Zealand were mapped to form the 'spatial dataset'. The spatial dataset provides an overview of all habitats that are known to contain *Cantuaria* populations and their respective environmental parameters. Population presence/absence data were collected during 2013-2016 field trips and from members of the public. Burrow sightings from the public were confirmed either by specimens collected from the area, or accurate *Cantuaria* burrow descriptions. The spatial dataset differs from the fine-scale dataset in the area covered and the data collected: the fine-scale dataset focuses on heavily localised parameters (e.g. soil pH) surrounding a small subset of South Island lidded *Cantuaria* populations. The fine-scale dataset also has equal numbers of presences and absences, as absences are taken from near the population where there are no burrows: it is therefore a dataset describing the differences between the middle of a population and the areas adjacent to it. Conversely, the spatial dataset covers all of New Zealand from Stewart Island up to Whanganui: the entire known range of *Cantuaria*. Data collected from the spatial dataset generally cover wider areas of land than the fine-scale dataset. For example, soil type (a variable included in the spatial dataset) is not likely to fluctuate as much as soil pH (a variable included in the fine-scale dataset) over a particular given area. The absences in the spatial dataset are independent from the presences. It is therefore a dataset describing the differences between regions where populations are present and regions where they are absent
.

To answer my second question, concerning the environmental factors relating to the presence or absence of *Cantuaria* populations, data was collected on environmental variables related to soil, vegetation, and climate-related parameters using both the comprehensive, low-resolution spatial dataset and the more specific, high-resolution fine-scale dataset.

To address my third question, concerning the effects of anthropogenic disturbance on *Cantuaria* population presence or absence, both datasets contained variables related to anthropogenic disturbance.

7.2.1 Data collection

Spatial dataset

All locations throughout New Zealand where *Cantuaria* burrows were found from 2013–2016 were plotted on an ArcGIS (Esri 2013) basemap. A different marker was used to denote areas where available habitat had been searched, but no *Cantuaria* had been found. All markers were placed in one ArcGIS baselayer (See Fig. 7.1).

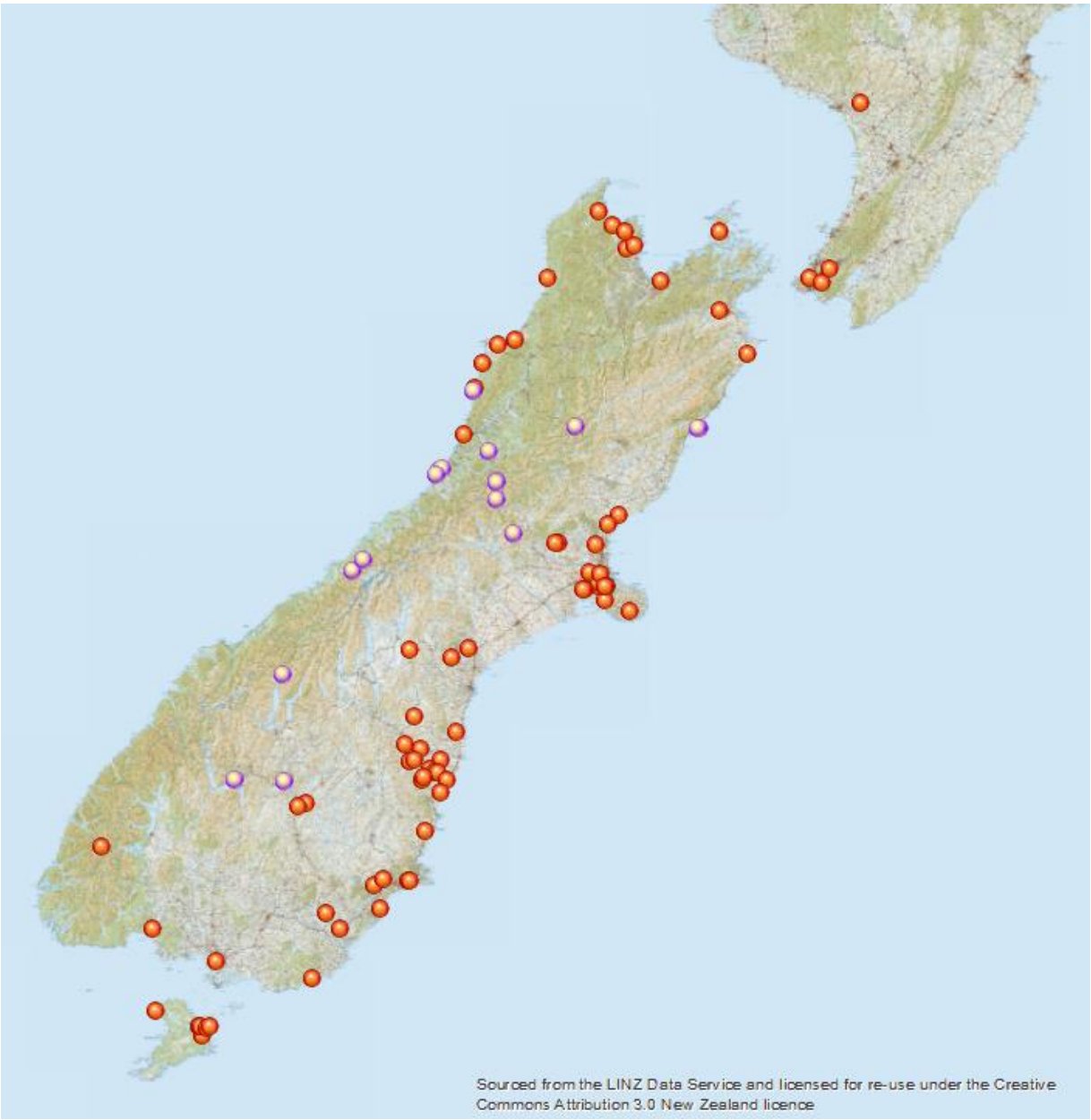

Figure 7.1: Map generated in ArcGIS showing the locations of *Cantuaria* populations. Presence of *Cantuaria* populations is indicated by the dark red markers, while light purple markers indicate areas that were searched without finding any *Cantuaria* populations.

Fine-scale dataset

While collecting *Cantuaria* specimens for phylogenetic and taxonomic analysis, I noted populations that appeared to have a definite population boundary that did not mark an obvious change in habitat. The usual high density of *Cantuaria* populations makes their boundaries quite obvious. If the unpopulated habitat appeared still suitable for *Cantuaria* (for example, the population was in one part of a clay bank but not another part of the same bank), I revisited the population later to collect data concerning possible parameters related to *Cantuaria* habitat requirements (see data collection section below). This fine-scale data provided information about specific populations, at a high resolution directly surrounding the localised population.

Due to the clustered structure of *Cantuaria* populations, a patch of habitat was considered to be inside a population if there was at least one burrow per 2 m^2. If no burrows were present within a 2 m^2 patch of habitat, the patch was considered to be outside the population. The 2 m^2 area was determined by a pilot study which found that, within a population, the density was almost always greater than or equal to one burrow per 2 m^2. At all population sites, I estimated percentage vegetation cover, vegetation type (1=native, 2= exotic), distance away from human impact (e.g. a road or farm), severity of human impact (1 = nature trail with little use, 2=more heavily used recreational area, farm or trail, 3=non-major road, 4=main road), and noted other details, such as the presence of tiger beetle larva (*Cicindela* spp.) burrows. Presence/absence, and density of burrows was noted. In addition, two samples of approximately 10 cm^3 of soil each were placed in ziplock bags for later moisture and pH analysis. Information was collected at four points around each population: two points where burrows were present, and two points where burrows were absent. Soil samples were collected at least two metres apart to reduce spatial autocorrelation, but since most populations present as a single large cluster on a clay bank, soil samples were taken from outside either side of the population, and from two points within the population that were at least two metres apart.

Soil processing

Soil samples were taken to measure soil parameters (pH and moisture content) by digging a 10 cm^3 hole with a trowel. At each population, soil samples were obtained at four sampling points (see data collection). Samples were stored in ziplock plastic bags at 8°C in the laboratory for up to one week before processing. From each population, four sets of two samples were collected; two sets outside the population, and two sets inside the population (see Fig. 7.2).

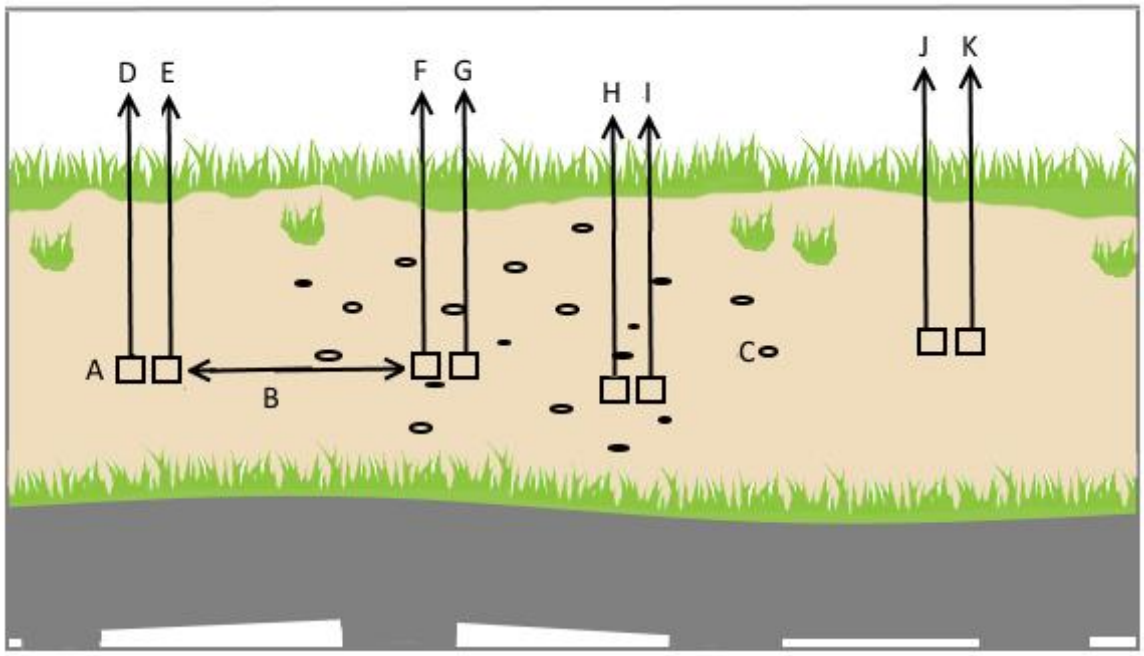

Figure 7.2: Diagram showing protocol for sampling soil from a roadside clay bank. A) Each square represents a 10cm^3 soil sample. Two squares together represent a set of two samples. B) Minimum of 2 m between sets of samples. C) Ovals represent *Cantuaria* burrows. D-K) One sample from each pair was air dried for pH testing; the other samples were oven dried to calculate moisture content.

Soil processing followed standard protocols (Blakemore, Searle & Daly 1987; Rayment & Lyons 2011). From each set of two soil samples, one sample was air dried for pH analysis and one was oven dried for moisture analysis. Soil pH was determined from a 10g crushed sample in solution with 25 ml deionised (DI)-water. The solution was then agitated by shaking and incubated for at least four hours. The incubated solution was agitated again before pH measurement with a pH meter (Mettler Toledo Seven; In-line Pro electrode). Moisture content was determined by weighing samples before and after oven-drying (at 80°C for four days) for subsequent calculation of percentage moisture.

7.2.2 Data analysis

The parameter value ranges at locations mapped in the spatial dataset were explored graphically using mapping, boxplots and bar charts to estimate the range of environmental conditions that support *Cantuaria* populations.

Environmental variables describing soil, vegetation, and climate-related parameters were modelled using mixed effect models implemented in R (R Core Team 2013) to identify the environmental factors relating to the presence or absence of *Cantuaria* populations.

Variables that related to anthropogenic disturbance (distance to anthropogenic impact, and type of impact) were included in fixed effects models to measure the effects of anthropogenic disturbance on *Cantuaria* population presence or absence.

Spatial dataset

Geographic information system (GIS) software (ArcGIS 10.3; Esri 2013) was used to assess *Cantuaria* population presence/absence over a much larger spatial scale, incorporating climatic and land use factors. Spatial data for land use were downloaded from the Land Cover Database (LCDB) (Landcare Research 2015). The LCDB contains information on vegetative cover and urbanisation, which are factors relating to human environmental modification and habitat type (questions 1, 2 and 3). Aside from land use, other environmental datasets included in the ArcGIS data analysis were mean summer temperature (°C) (LENZ 2015), annual mean temperature (°C) (Worldclim V. 1.4, Hijmans, Cameron & Parra 2005), soil type (using the New Zealand soil classification (NZSC) system; Landcare Research 2016), elevation (metres above sea level) (LINZ 2012) and annual precipitation (ml) (Worldclim V. 1.4, Hijmans et al. 2005). The datasets included in this analysis were chosen so that the environmental parameters that could potentially affect *Cantuaria* presence and absence could be modelled spatially.

A points layer was created in ArcGIS (Esri 2013) to map locations where *Cantuaria* were found throughout New Zealand from 2013–2015. Information on population locations was gathered during field trips and using data from NatureWatch ('NatureWatch NZ' 2014) and members of the public (where the spider specimens could be identified by the author as *Cantuaria*). If searching an area thoroughly did not reveal any *Cantuaria* burrows, the area searched was marked on the points layer as an absence.

After extracting environmental data to the points, a spreadsheet was created to list each point and its corresponding values from the datasets. The response variable was *Cantuaria* presence/absence, and five potential explanatory variables were assessed for inclusion in the model. The potential explanatory variables were mean summer temperature, mean annual precipitation, soil type, and land cover. Three different ranks (group, class, and order) of soil type were tested to decide which rank explained the most variation. Latitude, longitude, and point ID (the ID numbers given to the points marking *Cantuaria* presence and absences) were assessed for inclusion as random effects. Variables were tested for intercorrelation as for the fine-scale dataset. There were intercorrelations between latitude and land cover, latitude and soil class, and longitude and point ID. Mean annual precipitation was log transformed, as a histogram revealed it to have a Poisson distribution, not a normal distribution. A random forest decision tree was run using the randomForest package (Liaw & Wiener 2002), implemented using the Party package (Hothorn et al. 2010). The purpose of the random forest was to measure variable importance, taking into consideration any interactions and correlations (Boulesteix et al. 2012; Boulesteix et al. 2012). The random forest process ranked precipitation and soil class as being the variables with the highest importance. A set of general linear models (GLM) was then constructed with precipitation and soil class as the explanatory variables, and burrow presence as the response variable. Models were compared using Akaike's Information Criterion corrected for small sample size (AICc) values as with the fine-scale dataset, and the

effect of the explanatory variables on the response variable was assessed using p-values and pseudo r-squared analysis as for the fine-scale dataset.

Fine-scale dataset

For each location, mean values were taken before data analysis for the following variables: soil pH and moisture, impact distance, and vegetation cover. Mean values were used: one from inside the population and one from outside the population. The values were analysed in a GLMM without the need to add an extra random effect to avoid spatial autocorrelation.

GLMMs were constructed in R (R Core Team 2013) to examine variables that affect *Cantuaria* population distribution. First, explanatory variables (soil moisture, soil pH, vegetation cover, vegetation type, impact distance, impact level, and tiger beetle presence or absence) were tested for intercorrelations. The package Hmisc (Harrell Jr 2008) was used to test correlation coefficients for significance. Month was included as a random effect to avoid temporal intercorrelation. The response variable was *Cantuaria* burrow presence/absence. Competing, alternative mixed-effect models were constructed to assess the relative influences of potential explanatory variables. An intercept-only model, with no explanatory variables, was also constructed as a null model. The null model and all mixed-effect models were then compared to assess the relative effects of the explanatory variables compared to each other and the null model. To determine the amount of variation that could be explained by the explanatory variables, and which combination of variables explained most of the error, models were constructed using the lmer function in the R package lme4 (Bates, Mächler, Bolker & Walker 2015, p. 4). The models were ranked, using Akaike's Information Criterion corrected for small sample size (AICc), and their model-averaged parameter values were estimated. In this framework, the model with the lowest AIC value was considered to be the most informative (explaining the most variation in the response variable). Models within two AIC_c units of the top-ranked model were considered equally informative, but those with higher AIC values were considered relatively uninformative (Anderson 2008). The r.squared function, implemented using the MuMIn package (Barton 2013), was used to calculate pseudo r-squared values for each model, including both marginal and conditional coefficients of determination, to show the percentage of variation explained by the random and fixed effects (Barton 2015). For models without fixed effects, the ModEva package (Barbosa 2015) was used to calculate McFadden's R-squared values.

7.3 Results

Spatial dataset

The spatial dataset contained 89 points, including 72 presences and 17 absences. Populations of lidded-type *Cantuaria* (i.e. north of Dunedin) were mostly found in well-drained, sloping banks. The mean annual rainfall in areas where unlidded burrows were found was higher than the rainfall in areas where lidded burrows were found (Fig 7.3); however, sampling was biased

towards lidded burrows, with only 15 unlidded burrows, as opposed to 58 lidded burrows, found. Unlidded *Cantuaria* burrows were found mostly in damp, mossy or sparsely-covered soil. However, there were many populations found outside these conditions: lidded *Cantuaria* burrows were found in wet bush in Denniston and Charleston on the West Coast, and some unlidded *Cantuaria* were found in unforested, urban environments, such as Tuatapere in western Southland. Unlidded burrows were never found in dry, clay banks. Interestingly, unlidded *Cantuaria* burrows were found in damp sand on a Stewart Island beach, and in piles of semi-rotted seabird droppings on Whero Rock near Stewart Island. Despite the challenges these environments may pose (high salinity, high acidity, varying substrate texture), the population on Whero Rock was large (>20 individuals) and contained both juveniles and adults.

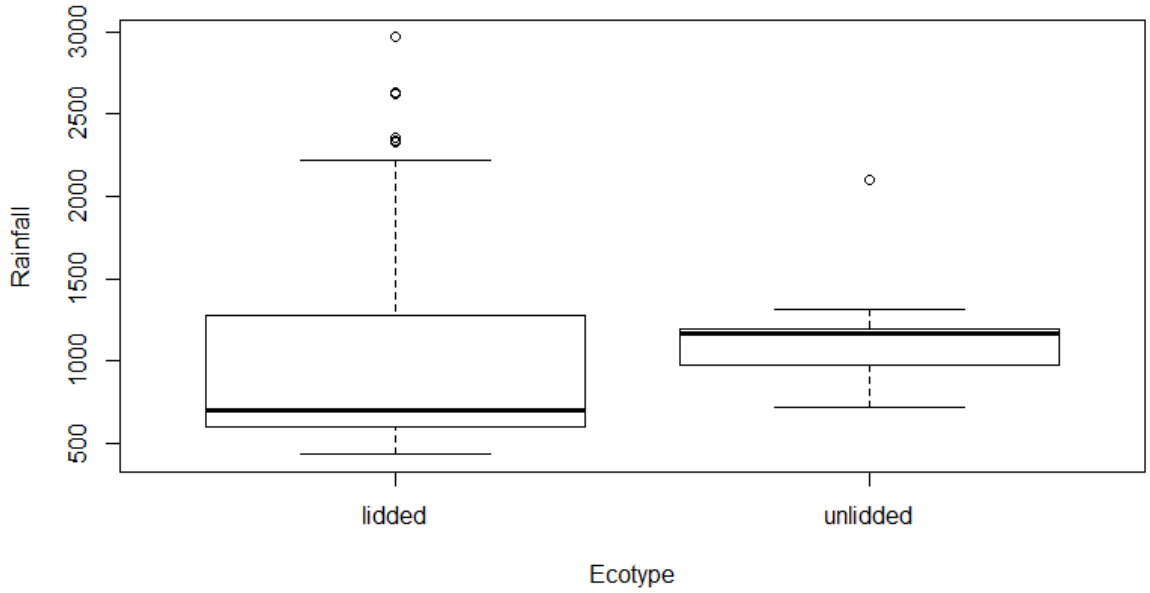

Figure 7.3: *Cantuaria* ecotype (lidded or unlidded) plotted against mean annual rainfall (mm).

The random forest analysis ranked soil group and mean annual precipitation as the highest contributing factors to explaining the variance in presence/absence of *Cantuaria* burrows (precipitation explaining 71.40% of the mean standard error, and soil group explaining 33.71% of the mean standard error (Fig. 7.4; note values do not add up to 100% as some error is explained by more than one variable). Other important variables were elevation (27.12%) and temperature (19.70%). Elevation and temperature were correlated (correlation coefficient -0.67, p=0.0003).

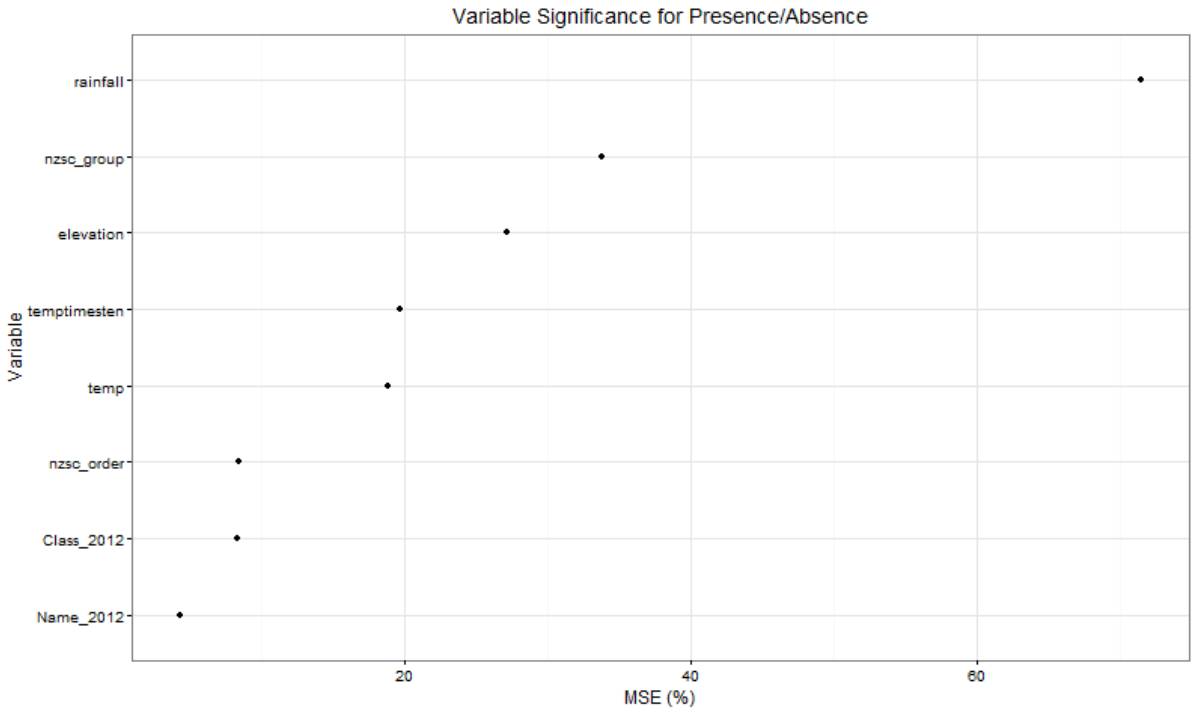

Figure 7.4: Scatter plot of mean standard error (MSE) explained by each of the variables tested. The plot was constructed using the R package ggplot2 (Ginestet, 2011).

The highest ranked variables (i.e. those that explained the most error) were included in different combinations in GLMs. Temperature was excluded due to its correlation with elevation, and the greater amount of error explained by elevation. The addition of random effects did not alter any of the output values, so they were left out of the models. The models and their corresponding AICc and P values are shown in Table 7.1.

Table 7.1: Fixed-effect models, their explanatory variables, and resulting AICc and P-values.

Model ID	Explanatory variables included	P-values	AICc
m1	Soil group Rainfall	1.0 <0.01	80.9
m2	Elevation Rainfall	0.06 <0.01	58.0
m3	Soil group Elevation Rainfall	1.0 0.11 <0.01	80.3
m4	Soil group Elevation	1.0 0.3	96.4
m5	Soil group	1.0	95.5
m6	Elevation	<0.01	81.0
m7	Rainfall	<0.01	59.9
null	Latitude	0.5	86

Models m2 and m7 had the lowest AICc values. Pseudo R-squared tests are shown in Table 7.2.

Table 7.2: Pseudo r-squared outputs for models m2 and m7.

	Model number	
Pseudo r-squared measures	m2	m7
Cox and Snell's	0.3237378	0.2940255
Nagelkerke's	0.5216366	0.4737612
McFadden's	0.403599	0.3592349
Tjur's	0.461835	0.4139589
Squared Pearson correlation	0.4768312	0.4252369

The relationships between the presence/absence of *Cantuaria* burrows, and precipitation and elevation, are illustrated by the graphs in Figs, 7.5 and 7.6. Most burrows found were present at medium-low precipitation levels, around 1000 mm/year; however, burrows were found in areas of high rainfall (up to 3000 mm/year). Most of the absences were in areas with rainfall of over 2000 mm/year, although there were some absences below 1000 mm/year. The correlation between low rainfall and *Cantuaria* presence appears quite strong in Fig. 7.5. A less pronounced correlation is evident in Fig. 7.6, which shows that most *Cantuaria* burrows were found at lower elevation, up to around 200 metres above sea level. No burrows were found above 750 metres. However, due to insufficient sampling in mountainous areas, the optimum elevation range for *Cantuaria* burrows cannot be postulated based on the data presented here. The optimum elevation may also fluctuate depending on latitude or other environmental factors.

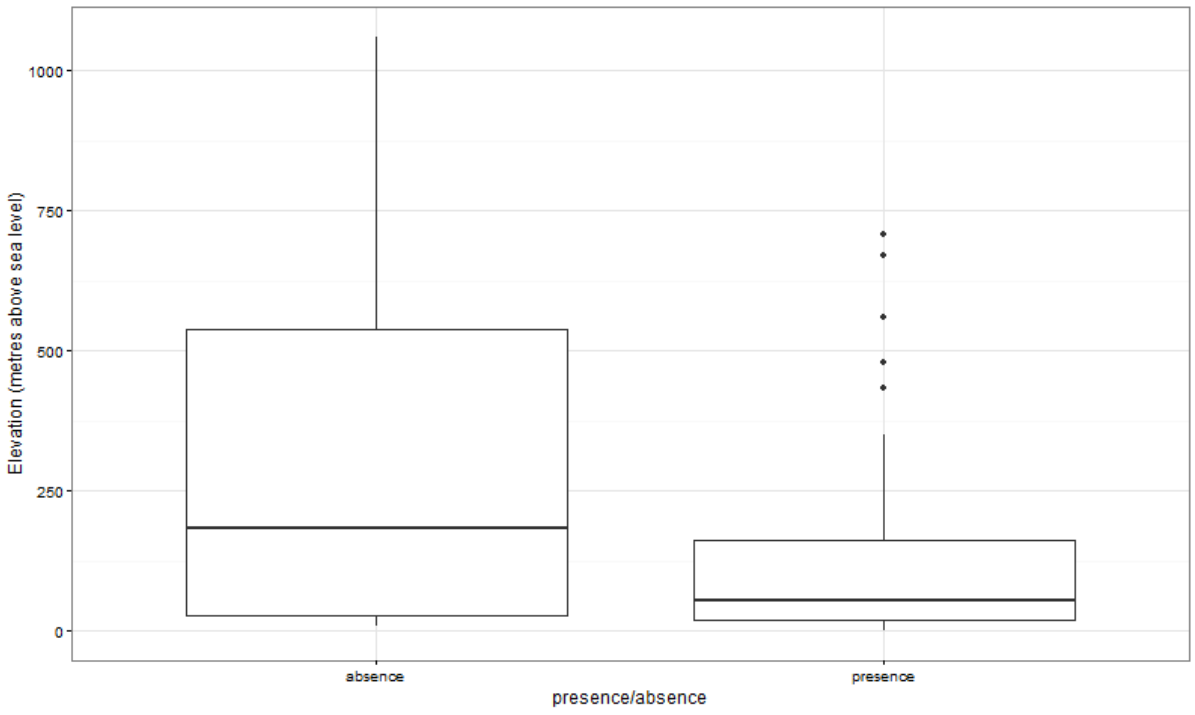

Figure 7.5: Presence/absence of *Cantuaria* burrows plotted against elevation.

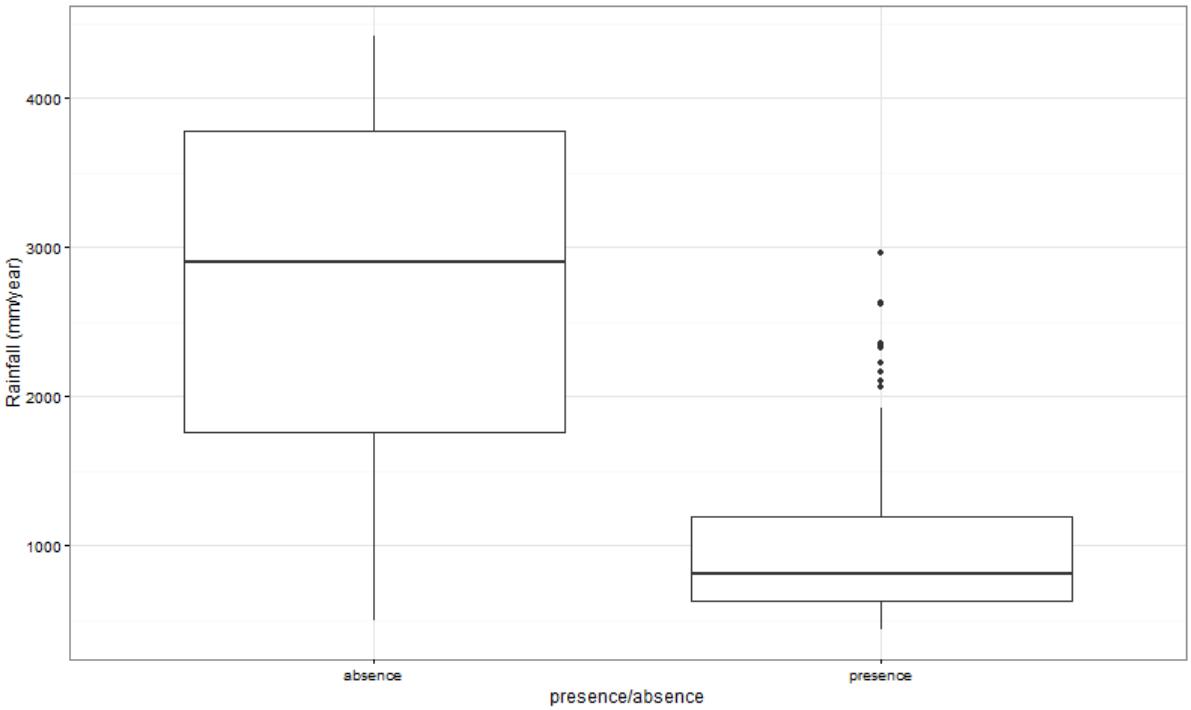

Figure 7.6: Presence/absence of *Cantuaria* burrows plotted against annual precipitation.

Fine-scale dataset

The fine-scale dataset contained 28 samples, with 17 presences and 17 absences. All sample populations included in the fine-scale dataset were north of Dunedin and containied lidded burrows only.

A set of linear models, described in Table 7.2, was constructed. There were correlations ($p < 0.05$ and correlation coefficients outside -0.7–0.7, or boxes not overlapping) between month, impact level, and vegetation cover. Running the remaining variables produced an error due to unidentified intercorrelation. Deleting variables by trial and error resulted in soil moisture, soil pH, and impact distance being included in the model as potential explanatory variables.

Table 7.3: Field data models and their associated test statistics.

Model ID	Explanatory (/fixed) variables included	P-values	AICc	R-squared
m1 (null)	Intercept only	1	40.82	0
m2	Soil moisture Soil pH Impact distance (Month)	0.80 0.75 0.79	48.6	0.01 (error: large eigenvalue)
m3	Soil moisture Soil pH Impact distance	0.81 0.76 0.81	50.43	0.01
m4	Soil moisture Soil pH Impact distance Month	0.82 0.77 0.81 0.99	52.41	0.01

None of the variables included in the models were significant or provided r-squared values above 0.4. The null model had the lowest AICc value. The variable with the lowest consistent p-value was soil pH (Fig. 7.7).

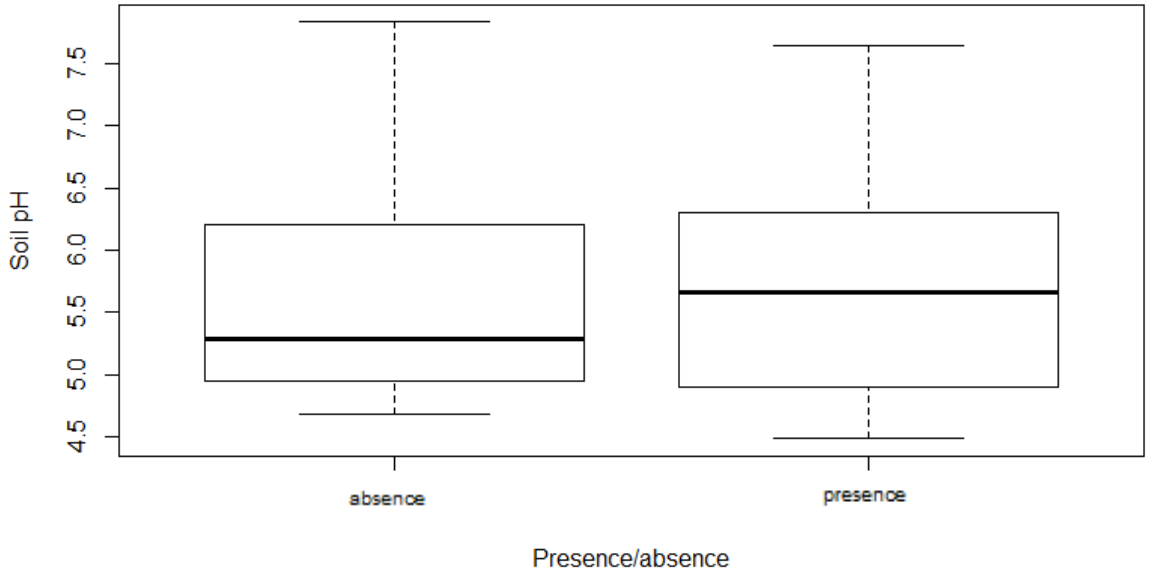

Figure 7.7: Soil pH plotted against presence/absence of *Cantuaria*.

7.4 Discussion

While the genus *Cantuaria* has been assumed to be a Gondwanan relict (Irish 2001), genetic evidence of many NZ endemic species that were previously assumed to have been relicts has shown that they are more likely to have dispersed over the Tasman Sea to New Zealand (e.g. Griffiths et al. 2005; Vink & Paterson 2003; Waters & Craw 2006). The research conducted for this chapter is intended to indicate the resilience or specificity of *Cantuaria* spp. to different conditions, and their ability to adapt to a variety of situations, which may provide some insight into any previous ability to survive a trans-Tasman journey, with possible subsequent colonisation.

My results suggest that *Cantuaria* spp. are able to withstand a surprisingly wide range of environmental conditions, considering their small population sizes and patchy distribution. The spatial mapping analysis revealed that mean annual rainfall and elevation appear to be the most important factors to the presence or absence of burrows. Rainfall and elevation are not intercorrelated. *Cantuaria* spp. appear to prefer areas with lower rainfall as no populations were found where rainfall is above 3,000 mm/year. Up to 1,000 mm/year appears to be the most favourable rainfall for *Cantuaria* spp. Unlidded *Cantuaria* spp. may prefer a higher mean annual rainfall, as rainfall was generally higher in areas with unlidded burrows compared to areas with lidded burrows (Fig. 7.3). *Cantuaria* also appear to prefer lower elevation to higher

elevation as no populations were found above 750 metres. The lower temperatures associated with higher altitudes (below 10°C in the Southern Alps, as opposed to above 10 °C outside the mountain range (based on data collected 1971–2000, NIWA 2006)) may limit the spread of *Cantuaria*. Additionally, soil and vegetation becomes sparser at high altitudes, which may limit both habitat and food abundance for *Cantuaria* spp. Mountain ranges may, therefore, pose a barrier to dispersal, possibly causing a split between east and west coast populations approximately 5 million years ago when the Southern Alps appeared (see Chapter 5). Rainfall and elevation are, however, the only important factors determining the distribution of *Cantuaria* that were found in this study. Other weak correlations included soil pH and soil group, but they do not appear to limit distribution. The wide range of soil types inhabited by *Cantuaria* spp. includes highly saline and acidic conditions, illustrating the ability of *Cantuaria* spp. to survive and reproduce in many different habitat types.

The results presented in this chapter should be taken into consideration when deciding which areas to conserve, or when developing *Cantuaria* management protocols. Areas with low rainfall, and at low altitude, appear to be ideal for *Cantuaria* populations to survive and reproduce; however, slightly higher rainfall may be preferred by unlidded species. More research is required to determine whether the habitat preferences of unlidded *Cantuaria* spp. differ from lidded species. Differences in habitat requirement are likely given the southern distribution of unlidded *Cantuaria* spp. Anthropogenic factors, such as roads and tracks, do not appear to affect *Cantuaria* distribution. However, anthropogenic climate change may have an effect on *Cantuaria* distributions: temperature and rainfall are both affected by anthropogenic climate change (NIWA 2016), although elevation is not. Annual mean rainfall is expected to increase on the West Coast, Tasman, Central Otago, and Southland areas (NIWA 2016), all of which have *Cantuaria* populations; the West Coast and Southland are of particular concern considering that they already receive high rainfall. An increased sea level (NIWA 2016) may also cause beach populations, such as those on Stewart Island, to move further up the beach. The individuals closest to the tide line may be killed by the salt water, unless they can leave their burrows and build another further up the tide line. Further research should be conducted into the ability of idiopids to react to change by leaving their burrows and building new burrows in desirable habitat.

The evidence presented in this chapter supports the biogeographical inferences made based on the dated phylogeny in Chapter 5. *Cantuaria* spp. do not seem highly sensitive to chemical variation in their environment, and can tolerate a wide range of environmental conditions including changes in temperature and moisture. Elevation and rainfall are important terrestrial factors, and must be taken into consideration when modelling distributions or developing conservation and management strategies. However, neither elevation nor rainfall would have been a strong limiting factor for the dispersal of *Cantuaria* from Australia to New Zealand. The ability to survive and reproduce under a wide range of environmental conditions has

contributed to the almost New Zealand-wide distribution of *Cantuaria*, and its success as a genus. Conditions inside a *Cantuaria* burrow may be more stable in temperature and humidity than ambient conditions; preliminary data collected by probes placed inside burrows, compared to probes inserted into the soil near the burrows, showed that temperature and humidity fluctuate less inside the burrows than in the surrounding soil (V. Smith, unpublished data). Burrows may therefore provide their inhabitants with protective buffering of conditions, possibly making a rafting scenario more plausible as the vehicle of transport of *Cantuaria* to New Zealand.

Future research into the ecology of *Cantuaria* could employ microsatellites or single nucleotide polymorphisms as a tool to assess connectivity of populations, and the ability of individuals to disperse over obstacles on land. Captive studies may also be useful to test the resilience of individuals to changes in salinity, moisture and temperature, and perhaps a long-term captive study could assess fecundity during periods of environmental change. Boosted regression modelling may also be a useful approach to predicting distributions, particularly with regards to future climate change.

Chapter 8
Conservation issues affecting New Zealand Idiopidae

8.1 Introduction

Arthropods have colonised most of the land area on Earth, diversifying into the most speciose animal phylum and filling a huge range of niches. Arthropods are important in every ecosystem in the world, but in large numbers they can also cause devastation to their environments and to human health and industry (i5K Consortium 2013; Nicholson 2007). Within the arthropods, spiders have evolved to become almost exclusively carnivorous, preying upon a variety of taxa including insects, crustaceans, and other members of their phylum. Spiders are vital arthropod predators in the vast majority of global ecosystems, from the fen wetlands of Britain to the alpine slopes of the Himalayas (Riechert & Lockley 1984; Wise 1995). They have expanded their diets to include annelids, molluscs, and even vertebrates, becoming extremely important to the structure and integrity of ecosystems worldwide (Wise 1995).

Spiders have diversified over time, developing a vast array of life histories, diets, and hunting styles (Foelix 2010). While most extant spiders, the Araneomorphs, live above ground, the two other spider infraorders (Mygalomorphae and Mesothelae) usually live underground. Among the most specialised fossorial mygalomorphs are the Idiopidae, or trapdoor spiders. Found throughout areas of the southern hemisphere ranging from tropical to (rarely) temperate, idiopids form dense, well-camouflaged populations which are perilous to terrestrial invertebrates (Irish 2001). Prey caught by trapdoor spiders are dragged underground, into burrows up to 40 cm deep, where the remains of prey items join spider faeces in nutrifying deep portions of the organic and surface soil horizons. Preliminary results show that soil near *Cantuaria* burrows has a higher carbon and nitrogen content than soil metres from the burrows (Appendix 1).

In addition to their roles as predators, idiopids are potential prey to many species of bird, rodent, and reptile. They are also important hosts to a variety of parasites, such as parasitic wasps, nematodes, and fungi (Irish 2001; Poinar Jr & Early 1990). Despite the ecological importance of idiopids, and their usefulness in controlling invertebrate pests, there is little research into their conservation and management.

Some important conservation issues have been raised surrounding Idiopidae. Like many other mygalomorphs, the life cycles of idiopids tend to be very long; they take several years to reach reproductive maturity (Inglis 2008), and the females in particular are long-lived (over 20 years in some species; Coyle & Icenogle 1994; Irish 2001; Marples & Marples 1972). Some species are known to exhibit egg-guarding and parental care of the spiderlings (Gupta et al. 2015; Irish 2001). One small (adults <15 mm) species, *Cantuaria huttoni*, was found to have only 18–20

eggs in an egg sac, each of which was 1.5 mm wide on average, and the spiderlings only began to move autonomously approximately one month after hatching. Egg sacs collected from Otago burrows usually contained 30 eggs or fewer (Marples & Marples 1972). Animals with a long life cycle which have a small number of offspring, and invest a relatively large amount of resources in each offspring, have slow-growing populations that recover slowly from any decline in numbers (Heppell, Caswell & Crowder 2000). These traits, in combination with a lack of ability to disperse, put idiopid species at risk of decline. Particular risk factors that may cause idiopid species to decline include habitat disturbance, or invasion by alien species. Idiopidae are not particularly well-studied, and a lack of scientific or media interest in their decline should not be taken as evidence that their populations are stable. There are no Idiopidae listed under the International Union for Conservation of Nature (IUCN) red list ('The IUCN Red List of Threatened Species' 2015), despite species such as *Aganippe castellum* being considered endangered by other authorities due to their lack of ability to recover from decline (Inglis 2008).

Idiopids show high degrees of local species endemism (Gillespie 2013; Opatova & Arnedo 2014), forming small, dense populations which grow slowly and have a greatly limited ability to disperse and overcome barriers (Raven & Wishart 2005; Rix 2013; Starrett & Hedin 2007). Additionally, the number of species within any particular idiopid genus is difficult to gauge without thorough molecular and morphological investigation, as Idiopidae are usually morphologically conserved and may form cryptic species complexes (Starrett & Hedin 2007). Habitat destruction, therefore, can vastly reduce or even exterminate entire species, even if only a small area is involved. Due to a low interest in taxonomic and general idiopid research, locally endemic species may already have been made extinct before they are even discovered; many small and apparently threatened populations exist, some of which may be new species (e.g. *C. insidia*, Chapter 6).

8.2 The genus *Cantuaria*

Cantuaria, New Zealand's idiopid genus, presents a case study in which to investigate the possible threats to idiopids worldwide. New Zealand idiopids exhibit a high degree of local endemism, long life cycles, and other life history traits typical of idiopids (Forster & Wilton 1968; Irish 2001; Marples & Marples 1972; Todd 1945). Unlike most other idiopid genera, however, the two New Zealand idiopid genera are found in temperate areas, and this must be taken into account when using them as an ecological case study. New Zealand Idiopidae are particularly speciose (42 species Natural History Museum Bern 2015, but see Chapter 6 for 12 potential new species and one potential new genus). *Cantuaria* are restricted to the islands of New Zealand, making them accessible to study without travelling to different countries to collect specimens. Much of their habitat is degraded or threatened, and studying *Cantuaria* will increase our understanding of how Idiopidae respond to habitat destruction and degradation.

In this chapter, I examine the potential conservation issues affecting *Cantuaria* in light of recent research, and extrapolate these findings to explore what they may mean for the Idiopidae family as a whole.

Previous research on the Idiopidae of New Zealand (three papers, a monograph, taxonomic work, and a book) focuses little on potential conservation issues that may surround them. The three papers (Marples & Marples 1972; Poinar Jr & Early 1990; Todd 1945) mention short-range endemism, slow reproductive and growth rates, and lack of dispersal ability, but do not speculate about possible conservation issues that may arise from these traits. The monograph (Gillies 1875) gives a comprehensive anecdotal account of the burrows, distribution, and behaviour of New Zealand trapdoor spiders, but does not speculate about potential threats to their survival. The book, by Irish (2001), gives a more extensive (but mostly anecdotal) account of conservation issues. All previous literature focusing on *Cantuaria* describes them as likely to form distinct populations which are connected genetically by males during their seasonal dispersal periods. Species are therefore assumed to be limited by the distances males are able to cover (Irish 2001; Poinar Jr & Early 1990; Todd 1945). Forty-two species of *Cantuaria* have been described based on morphology, from *C. wanganuiensis* in the North Island to *C. stewarti* on Stewart Island (Forster 1968; World Spider Catalogue 2015). Chapter 6 of this thesis presented evidence that the described species may fall into two genera, which may in future result in the removal of the 13 *huttoni* group species from the genus *Cantuaria* into a separate (as yet undescribed) genus. All *huttoni* group specimens that were sequenced (*C. stewarti*, *C. sylvatica*, *C. delli*, *C. apica*, *C. catlinensis*, and *C. orepukiensis*) fell into a separate clade which is genetically, morphologically and ecologically distinct from the rest of the genus *Cantuaria*. However, the variable placement of *C insulana* (supported by low clade credibilities) prevented the new genus from being confirmed in this thesis. Future research is likely to result in the splitting of *Cantuaria* into two genera.

Chapter 6 also presents evidence for 12 new *Cantuaria* species. The high speciosity of the genus *Cantuaria* is attributed to the limited dispersal ability of individuals, combined with the assumption that *Cantuaria* spp. have been present in Zealandia since it split from the rest of Gondwana (Irish 2001; Poinar Jr & Early 1990). The proposed two genera inhabit different regions of New Zealand, and are subsequently likely to have different habitat requirements. The species boundaries I have designated reveal that, while some species are spread throughout a large area (e.g. *C. fountainae*), others may only be represented by a small number of populations (e.g. *C. hithaeglirensis*). More populations are likely to be found in the future, but they may be at risk from building or landscaping, or there may only ever have been one or two populations.

Irish (2001) mentions the topic of conservation regularly throughout her book; her concern for the future of individual populations is obvious. Irish (2001) has a chapter describing the threats to a particular population of *Cantuaria* spp. found in Kakanui. The Kakanui population builds

trapdoors in cliffs over the estuary (possibly taking advantage of the insects basking in the sun on the cliff face), which constantly erode. Irish believes the population cannot recede from the cliffs as they erode. The population has decreased in size with cliff erosion at least since the 1960s, and Irish perceives the existing threat to be exacerbated by human development and disturbance from cultivation and modification of cliffside grassland habitat. Translocation of the spiders, and prevention of further disturbance, is suggested as part of a community-based conservation plan proposed by Irish (2001). Chapter 4 of this thesis describes a method (beetling) of removing specimens from their burrows without damaging or killing them; beetling could be used to translocate spiders that inhabit highly disturbed areas. Irish does not consider that *Cantuaria* near cliffs are likely to regularly encounter erosion, and their populations may move away from the eroding surface as it falls. Also noted are the naturally small sizes of *Cantuaria* populations, and the possibility that they could easily become isolated by human activity and consequently driven to extinction. Irish assumes that *Cantuaria* populations could be isolated by geographic distance alone (Irish 2001).

The purpose of this thesis is to investigate the biogeography and ecology of *Cantuaria*, both of which are closely related to conservation issues. I have built upon previous work and anecdotes described by Irish (2001), by investigating the effects of environmental parameters on idiopid presence throughout New Zealand (see Chapter 7). The results of the habitat study can inform future conservation management plans by showing which areas are of greatest importance to conserve for New Zealand idiopids. In particular, I found that rainfall, and possibly elevation and temperature, affect idiopid presence or absence. As rainfall and temperature in New Zealand may be affected by climate change (NIWA 2016), some idiopid populations may not be able to adapt to higher rainfall or temperature; as a result, large-scale population extinction and perhaps species extinction may occur.

Finally, my biogeographic analysis has shown that, while *Cantuaria*'s presence on New Zealand is likely to be the result of a single long-distance dispersal event, *Cantuaria* is dispersal limited and has mostly spread very slowly northwards from the south of the South Island (see Chapter 5). Gene flow between populations on either side of barriers (such as bodies of water or mountains) is likely to be highly restricted. If town or city development represents a barrier, gene flow may be lost between populations on either side of the development; however, the loss may not be detectable until many years in the future due to the long life cycle of *Cantuaria*.

8.3 Suggestions for management

Soil moisture, soil pH, nearby anthropogenic activity, and vegetation type do not appear to affect presence or absence of *Cantuaria* (see Chapter 7). The findings in Chapter 7 should be interpreted with care, as the study did not look at individual species, and unlidded Idiopidae were underrepresented. However, rainfall does appear to affect *Cantuaria* distribution, and future research may reveal that elevation, temperature and soil type may also affect population

presence or abundance. These parameters must be taken into account when identifying an area for the protection of *Cantuaria* spp. A piece of land at low elevation, with low rainfall is a preferable reserve to one with high elevation and high rainfall, all other factors being equal. Although *Cantuaria* spp. are in general abundant and not considered threatened, some species (such as *C. insidia*) may be threatened. Future surveying may reveal threatened species in this genus, and reserves may be necessary to conserve those species. Further, climate change in New Zealand is likely to alter rainfall patterns (NIWA 2016), and some species may decline as a result of increased rainfall. These species may need protection, or taking into captivity as part of a captive breeding program. Some areas, such as the east coast, may receive less rainfall and become more habitable by *Cantuaria*; the populations already in these areas may be able to expand and possibly speciate as they colonise a greater area, but they may also be threatened by other issues such as urbanisation.

Cantuaria spp. are well-suited to conservation by land protection, as their small populations would remain in the reserve and any change in distribution would be over long periods of time (Irish 2001; Marples & Marples 1972). While individual males or parasitised females may leave the reserve, the nucleus of the populations would remain, changing only very gradually (Marples & Marples 1972). Human activity would be possible within the reserve as long as the soil was not uplifted. My research (Chapter 5) did not illuminate whether habitat corridors might be useful to connect populations via male gene transfer. Threats to wandering males are likely to be by predation, drowning, or humans killing individuals due to their propensity to wander into human dwellings. Large wandering males appear frightening to some humans, and are very conspicuous to humans and possibly other mammalian predators. Placing signs around developed areas throughout New Zealand during wandering periods (mostly autumn and winter), and using social media to spread information, may help to raise awareness and prevent some spider mortality. Additionally, builders and landscapers occasionally unearth populations of *Cantuaria* spp.; I was often contacted regarding unearthed spiders during the course of this study. One landscaper unearthed 35 adult female and male spiders from a single population, some of which had juveniles in their burrows. Whether or not the spiders were translocated is unknown. Spreading information about trapdoor spider populations, and suggestions for improvement of their survival prospects after unearthing, may prevent some populations from going extinct. For example, new holes could be made in the ground and the unearthed spiders placed inside them, as found to be effective in captive management (see Appendix 1; S. Cook, pers. comm.).

8.4 Suggestions for future research

Threats to *Cantuaria* populations include habitat loss from climate change, urbanisation, and physical disturbance of soil. The presence of *Cantuaria* populations with numerous adults and juveniles in the middle of urban areas, such as Christchurch and Oamaru, indicates that, under some conditions, habitat loss does not destroy *Cantuaria* populations. Populations appear able

to survive and reproduce under a wide range of environmental conditions (Irish 2001, see also Chapter 7). Future research should aim to determine which conditions are necessary for the survival of *Cantuaria* populations in urban areas. More thorough, species-specific ecological study is now possible due to my taxonomic and phylogenetic analysis. However, molecular methods should continue to be employed to increase our understanding of gene flow between populations. Microsatellites or single nucleotide polymorphisms (SNPs) could be combined with harmonic radar, radio tracking, or passive integrated transponder (PIT) tagging to study male movements along and between patches of habitat. The large *C. johnsi* or *C. mcquillanii* males could possibly carry small transmitting devices, such as those designed for insects (ATS 2015; Hamilton 2008; Stockan & Robinson 2016).

Cantuaria spp. are unusual idiopids: they inhabit areas with a temperate climate (most idiopid species are tropical; World Spider Catalogue 2015), have adapted within a single genus to a wide range of habitat types, and have undergone oceanic dispersal (Chapter 5). However, their population structure and life histories are very similar to those of other idiopids (e.g. *Idiops joida;* Gupta et al. 2015). My results may indicate conservation issues faced by idiopids in other regions of the world. Further study should be conducted to find out whether other idiopids show similar sensitivity to weather patterns and climate, and similar resilience to soil and vegetation parameters. One Indian species, *Idiops joida*, is known to prefer sparse vegetation and steep slopes (Gupta et al. 2015), so there are likely to be some differences between species depending on the habitat types to which they are adapted. Idiopid species are often found to be locally endemic (Gupta et al. 2015; Opatova & Arnedo 2014; Raven & Wishart 2005; Rix 2013), and there are likely to be undiscovered species in rural areas around the tropical regions of the world. These species may be threatened by habitat destruction and climate change in similar ways to *Cantuaria* spp., but until future research can be conducted, the effects of anthropogenic changes cannot be fully understood.

The current thesis has found that most *Cantuaria* spp. are likely to be largely resilient to small changes in their habitat, and over time may be able to overcome small barriers to gene flow. Whether or not this resilience is reflected in other idiopid species has yet to be determined. Conservation of habitat patches where idiopid populations are found is vital to their survival, as is prevention of uplifting soil within potentially threatened populations. Awareness must be raised amongst people who live in countries where Idiopidae are found, as humans are most likely to come into contact with males, which appear to represent the only form of gene flow between populations. Many New Zealanders are unaware that such large, impressive spiders exist in New Zealand, or that they build trapdoors and have a long life-history. Raising awareness in New Zealand about its endemic Idiopidae may improve future survival prospects for *Cantuaria*, and increase public understanding and appreciation for native spiders and wildlife in general.

Chapter 9
Concluding discussion

9.1 An unexpected journey

My research, presented in this thesis, intended to uncover the biogeographic history of the genus *Cantuaria*. I had particularly aimed to investigate whether *Cantuaria* had dispersed to New Zealand or remained on Zealandia after it split from the rest of Gondwana. To achieve my aim, I collected phylogenetic evidence to identify the approximate date at which *Cantuaria* diverged from its sister genus, *Misgolas* (Chapter 5). The phylogeny also enabled me to track *Cantuaria*'s historic distribution throughout its radiation period, enabling assessment of the genus' dispersal ability. To corroborate the phylogenetic evidence, I collected ecological data to determine how plausible an oceanic crossing would be for *Cantuaria* (Chapter 7).

Initially, I had hypothesised that *Cantuaria* would be a "ghost of Gondwana", having survived on Zealandia as it floated to its current position and became almost entirely submerged. Unexpectedly, phylogenetic evidence suggested that *Cantuaria* dispersed across the Tasman Sea approximately 18 million years ago (Chapter 5). Ecological evidence supports the possibility that *Cantuaria* could have successfully colonised after trans-oceanic dispersal, as they can survive and reproduce under a wide range of conditions (Chapter 7). I had not expected to conclude that *Cantuaria* is most likely to have dispersed, but perhaps it was not so unlikely, given the strong evidence supporting trans-oceanic dispersal for many flora and fauna, including those that currently have little dispersal ability (Chapter 3).

9.2 New Zealand biogeography

Popular opinion continues to perpetuate vicariance, rather than dispersal, as the driving force behind New Zealand's current biota. Television (e.g. BBC 2016) and books (e.g. Meyer-Westfeld 2014) continue to state that New Zealand's biota has been isolated from the rest of the world for 80 million years (since Zealandia split from Gondwana). The high degree of endemicity of New Zealand's species, and their unique adaptations, appears to support the idea that they have diversified independently from the rest of the world due to their isolation. The genus *Cantuaria* was also thought to have a vicariant history (Irish 2001), partly due to its low dispersal ability (Forster & Wilton 1968; Irish 2001; Marples & Marples 1972). However, my research has produced evidence that *Cantuaria* dispersed to New Zealand after it emerged post-Oligocene, adding to the growing body of evidence that low vagility does not preclude long-distance dispersal.

Some evidence suggests that most of New Zealand's biota, including trapdoor spiders, dispersed from Australia post-Oligocene (Chapter 3). A Gondwanan vicariance history is

strongly supported for some lineages (e.g. Boyer & Giribet 2009; Giribet & Boyer 2010), and others appear to have dispersed to New Zealand after the Gondwanan breakup but before the Oligocene drowning (e.g. Teeling et al. 2005). New Zealand biogeography should therefore not be split into advocates of dispersal and advocates of vicariance; the rich biogeographical history of New Zealand has supported both dispersal and vicariance, including in-between scenarios (Chapter 3).

A common misconception holds that dispersal-limited species, such as flightless birds and invertebrates, are unable to undergo long-distance dispersal. However, even non-vagile lineages can surprise us with their unexpected histories of dispersal: even sessile organisms can be carried by rafts of driftwood and debris, as long as a small number of individuals can survive the changes in climate and habitat. Kiwi (Mitchell et al. 2014), spray-zone spiders (Opell et al. 2016), kauri tree (Biffin et al. 2010), and skinks (Chapple et al. 2009) are all dispersal-limited lineages, but evidence suggests that they survived a long-distance dispersal event from Australia to New Zealand. *Cantuaria* is an excellent example of a dispersal-limited lineage having undergone long-distance dispersal, suggesting that New Zealand is both "Moa's Ark" (Bellamy et al. 1990) and the "Flypaper of the Pacific" (Dawson & Winkworth 2008; Didham 2005). New Zealand contains some ancient Gondwanan taxa, and some taxa that have arrived there more recently.

9.3 The contribution of this thesis to science

The research presented in this thesis has increased our knowledge concerning the biology of New Zealand idiopids. Biogeography and ecology, the focal points of this thesis, are intrinsically linked with taxonomy and conservation (Russello & Amato 2004; Whittaker & Fernandez-Palacios 2007). In Chapter 6, I revised the taxonomy of the genus *Cantuaria* to gain knowledge regarding genetically distinct species and their distributions. I found evidence that the genus *Cantuaria* consists of two morphologically, genetically, behaviourally, and ecologically distinct genera. A new genus within the family Idiopidae increases our knowledge of New Zealand's biodiversity, and opens avenues of research into the biology of the two genera. New Zealand idiopid genera may require different conservation management plans due to their different distributions and ecology. Combined with the habitat selection results in Chapter 7, the new taxonomy information could be used as part of a conservation management plan for any *Cantuaria* species that are deemed at risk. Most *Cantuaria* populations were found to be large and contain many adults and juveniles, but some conservation concerns were raised in Chapter 7. In particular, severe soil disturbance (such as quarrying or landscaping) may threaten populations of *Cantuaria* (e.g. *C. insidia*). Some *Cantuaria* populations are very small (Irish 2001; pers. obs.) and may be declining. The dense, patchy nature of *Cantuaria* populations could conceivably increase the threat from intensive localised human activity such as digging, as digging in only a small area of land could unearth many individuals. Since *Cantuaria* species

cannot be reliably distinguished using morphology (Chapter 6), entire species may begin to decline even before they are described.

The discrepancy between morphology and genes with regards to *Cantuaria* taxonomy (Chapter 6) has contributed to current understanding of genes versus morphology in taxonomy (Bond et al. 2001; Cranston et al. 2010; Emata & Hedin 2016; Hebert et al. 2003; Lefébure et al. 2006; Satler et al. 2013 2011; Will, Mishler & Wheeler 2005), by illustrating how genes can help to clarify a taxonomic conundrum. While animal morphology and genes often produce largely concurrent phylogenies (Carrasco et al. 2012; Giribet, Edgecombe & Wheeler 2001; Vink & Paterson 2003), genetic phylogenies will frequently show different evolutionary relationships than those retrieved using morphology alone (Belfiore et al. 2003; Emata & Hedin 2016; Lefébure et al. 2006). Some researchers regard the discrepancy between molecules and morphology as a sign that DNA is unsuitable for taxonomy (e.g. Will & Rubinoff 2004); others regard DNA as another character, to be used alongside morphology in taxonomy (Baker et al. 1998; Doyle 1992). However, molecular taxonomy is being used more frequently and has proven useful in species delimitation, particularly where cryptic species are present (Belfiore et al. 2003; Hamilton et al. 2011; Starrett & Hedin 2007). The benefits of molecular analysis has led to some advocates proposing its use as the main indicator of species and taxonomic relationships (Blaxter 2004; Tautz et al. 2003). In my research, DNA taxonomy has been useful in delimiting and identifying species boundaries in a genus with ambiguous morphology.

Molecular taxonomy has been used to delimit idiopid species in this study and other studies (Opatova & Arnedo 2014; Rix 2013), but collecting samples can be difficult. Sampling involves digging up spiders (which is labour-intensive and destroys burrows) (e.g. Mirza & Sanap 2012) or pitfall trapping (which catches only males) (Engelbrecht 2013). Previous methods of extracting trapdoor spiders from their burrows result in the death of the specimen, or the destruction of its burrow, which may leave it vulnerable to predation. In the current thesis, however, I discovered a highly successful technique using tethered beetles to capture trapdoor spiders (beetling; Chapter 4). Beetling does not damage the specimen, and only causes destruction to the topmost portion of a burrow, which can easily be reconstructed if necessary to replace the specimen. Future developments of non-destructive DNA techniques may enable molecular (and possibly some morphological) taxonomy to be studied without harming the specimens sampled, or removing them from the breeding population. Sampling without killing specimens would be beneficial in many mygalomorph families, particularly where species ranges are not known, or there are known or suspected endangered species.

The main limitations of the research presented in this thesis surround the incomplete DNA sampling. Prior to the commencement of my molecular work, few known primers were available for molecular analysis in mygalomorphs. Of the four known useful primer sets, only three proved useful to any degree in *Cantuaria*. Near to the end of my molecular research, three new primer sets were developed specifically for Idiopidae (M. Rix, pers. comm.). The new

primers were developed as part of a family-level study into Idiopidae evolution and biogeography, using next-generation sequencing (NGS) to develop suitable primers so that large numbers of individuals could be sampled to create a comprehensive phylogeny. If I had used NGS, my research may have taken more time and resources, but I would likely have been able to construct a more comprehensive phylogeny. In particular, I would have been more able to resolve some of the relationships within the genus of unlidded New Zealand idiopids that remain ambiguous. Sequences from the unlidded idiopid species were particularly difficult to obtain. Using NGS may also have enabled me to obtain single-nucleotide polymorphisms (SNPs) so that between-population relationships, including population and landscape genetics, may have been studied.

If more time and resources could have been allocated to the ecology research conducted for this thesis, more systematic data collection could have been conducted. For example, dividing a map of New Zealand into equal-sized areas, and randomly selecting areas to search for populations, may have given a more accurate idea of where populations are present and absent. More even coverage of New Zealand would reduce bias caused by intensively searching areas that are accessible, e.g. tramping tracks and roadsides. However, such a study would still carry bias: much of New Zealand is dense bush, which is difficult to search for trapdoor spiders (pers. obs). Combining the search with a pitfall trapping program may have facilitated the discovery of cryptic populations, resulting in greater collection coverage of the genera and consequent deeper understanding of their taxonomic structure. A higher resolution, less biased dataset would also give the ecological models more explanatory power. The need for air transport, and increased time allocation, would have made this approach unfeasible for the current study; however, future research may consider this approach when surveying New Zealand biodiversity, and include trapdoor spiders in the survey.

9.4 Future avenues of research

Any study that builds upon the foundations laid by my research should expand its sampling efforts to include oceanic islands that were unrepresented in my dataset. Collecting from island populations would facilitate greater understanding of how *Cantuaria* species spread, and the frequency of ocean crossings. Further, there are probably new species and possibly even new genera to be found on oceanic islands. The genetic distances between *C. stephenensis* (Forster, 1968) and *C. insulana* would be particularly interesting to discover, as *C. insulana* forms a clade with *C. viridiensis* that is sister to most of the remaining *Cantuaria* species (Chapters 5 and 6). *Cantuaria stephenensis* is geographically closer to *C. insulana* than *C. viridensis* is, but whether or not genetic distance equates to geographic distance in this group would further reveal the nature of *Cantuaria* dispersal. By optimising the beetling technique (Chapter 4) to enable non-destructive sampling, many more individuals could be DNA sequenced without impacting population vitality.

Minor studies that I conducted outside of the major topics of this thesis could serve as preliminary data for further research. For example, the data describing soil nitrogen and carbon content (Appendix 1) indicate a possible increase in soil nitrogen and carbon near *Cantuaria* burrows. A larger dataset could include soil samples from more populations, and careful selection of where the samples are taken (for example, a transect leading through a population to many metres away from that population). The larger dataset would enable calculation of the effect of individual *Cantuaria* burrows, and whole *Cantuaria* populations, on soil carbon and nitrogen content. A captive study could also be conducted to ensure that the different carbon and nitrogen levels are not artefacts of *Cantuaria* habitat selection. Uncovering positive effects that *Cantuaria* populations have on their environment could improve public perception of trapdoor spiders, and encourage farmers and gardeners to protect populations on their land.

Cantuaria venom would be an ecologically and medically interesting subject for further study (Appendix 5). Although no data were gathered, the larger *Cantuaria* were easy to milk for venom, and a Bradford assay suggested the venom was highly concentrated. Beetles that were occasionally bitten by *Cantuaria* usually remained alive for at least 24 hours after the bite, but a beetle bitten by an individual from one population in Johnsonville died immediately. The quicker death may have been due to organ penetration or previous pathology, but it may also have been due to stronger venom components injected by the spider. *Cantuaria* venom may have medical implications; LD50 tests conducted on a selection of prey items during a selection of time periods could reveal the strength, potency and fluctuating properties of the venom compounds.

The research presented in this thesis has advanced our current understanding of the ecology, biogeography, and taxonomy of New Zealand Idiopidae. The 21 other idiopid genera (World Spider Catalog 2016) also show high degrees of local endemism and cryptic speciation (Opatova & Arnedo 2014; Rix 2013), and they inhabit tropical and subtropical areas that are heavily disturbed by humans (Engelbrecht & Prendini 2011). Further research into idiopid ecology and taxonomy would improve our understanding of the issues that idiopid spiders may face both presently and in the future. Research on idiopid genetics and taxonomy has revealed issues in using their morphology for taxonomy (Engelbrecht & Prendini 2011; Opatova & Arnedo 2014), and *Cantuaria* is an example of a genus with complex discrepancies between morphological and molecular data. Research into the taxonomy of other idiopid genera may reveal widespread complexities and cryptic species; combining this knowledge with research into idiopid ecology would enable more inferences to be made regarding conservation and global biodiversity (Engelbrecht & Prendini 2011; Opatova & Arnedo 2014).

Further research on biogeography, both globally and focusing on New Zealand, should take into account that even dispersal-limited species can disperse long distances if given enough time (Chapter 3). The processes and factors leading to dispersal in dispersal-limited species require further research, as does the time taken for taxa with differing dispersal abilities to disperse.

9.5 Over the hill and across the water: Conclusion

My thesis describes the evidence that New Zealand Idiopidae are dispersal-limited spiders that, nonetheless, have dispersed over the Tasman Sea to New Zealand. During my research I have mapped their movements from Southland northwards, to reach their current wide distribution and high number of species. The discrepancy between *Cantuaria* morphology and molecular data, combined with the indication that there are more idiopid genera in New Zealand than originally suspected, invites further research into their taxonomy and ecology.

Cantuaria carries the distinction of being the only idiopid known to have undergone long-distance oceanic dispersal, and despite its endemicity to a small group of islands, it is the third most speciose genus within the family Idiopidae. *Cantuaria*'s natural history is therefore an illustration of the diversity and distinctiveness of New Zealand species, regardless of whether or not they dispersed from Australia.

End

""I come from under the hill, and under the hills and over the hills my paths led."

– The Hobbit, J. R. R. Tolkein

Appendix A
Observations of the natural history of *Cantuaria* spp.

A.1 Burrow structure

In two populations (one unknown species in Yaldhurst and one *C. curtisi*), plaster casts of spider burrows were made by pouring plaster of Paris (Hils & Hembree 2015) down five holes. The plaster was left to set for 24 hours before being unearthed with a shovel. Plaster of Paris burrow casts were examined to see the general burrow form, and compare how much variation could be detected within the sample, Burrow casts were compared with previously hypothesised burrow forms (Irish 2001) to form a preliminary investigation into burrow structure.

Burrow casts are shown in Figure A1.1. The burrows tested were up to 25 cm deep, with the largest non-branching cross section 21 mm in diameter. The burrows were slightly crooked, not straight, and one of them had a single side chamber. Remains of food items were often found in the bottom of the burrow attached to the plaster.

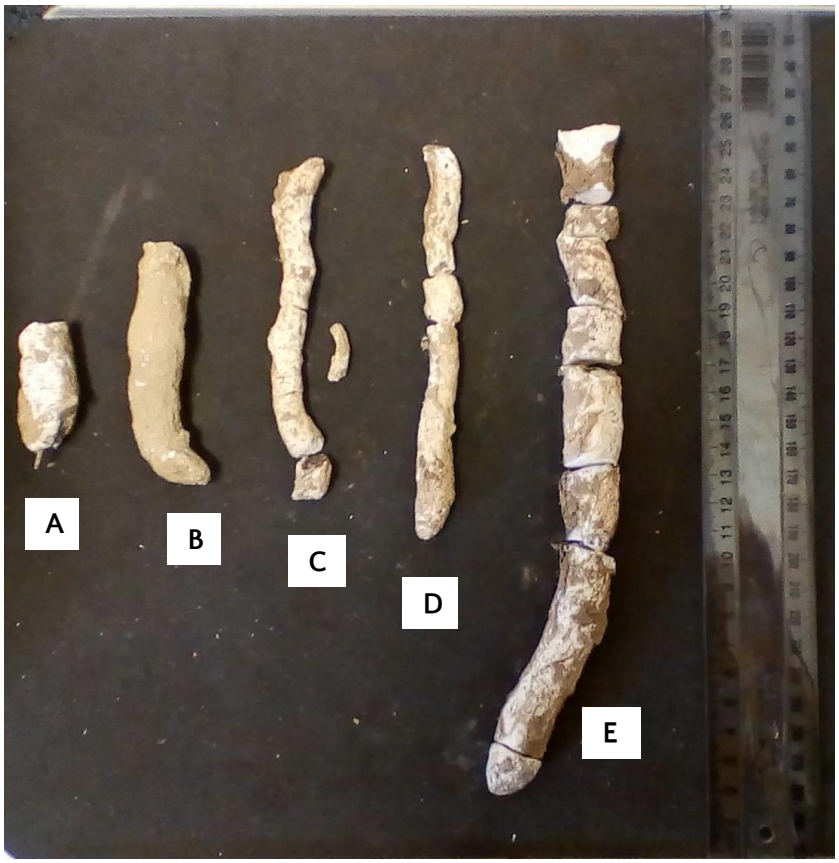

Figure A1.1: Plaster of Paris casts of *Cantuaria* burrows with a 300 mm rule for size context. A) incomplete Yaldhurst burrow; B) complete Yaldhurst burrow, unbroken; C) complete Yaldhurst burrow, broken, with side branch and food remains at the bottom; D) complete Yaldhurst burrow, broken; E) complete *C. curtisi* burrow, broken. The side branch of burrow C is difficult to place along the burrow, as there is no obvious breakoff point. Broken burrows were reassembled by placing interlocking pieces together. However, the order of pieces may be incorrect.

The burrows uncovered varied in depth and width, but largely matched descriptions by Irish (2001). Irish described them as simple burrows of varying depth (15–49 cm) and occasional other structures such as bellies (wider portions of the burrow, perhaps to allow the spider to turn around) and branches. Irish also noted that the tops of burrows were usually slanted, as seen by 3) and 4) in Fig. A1.1. *Cantuaria* burrows have a simple and variable structure, but revealing more about their depth may aid in assessing the impact that populations have on the surrounding soil, as deeper burrows may bring nutrients from discarded prey remains deeper into the soil (see A1.2). Future studies could use resin instead of plaster (Atkinson & Chapman 1984), as digging plaster out of burrows without it breaking is difficult. Unearthing deep burrows in hard clay soil would be almost impossible by hand.

A.2 The effect of *Cantuaria* presence on soil nitrogen and carbon

Soil nitrogen and carbon are indicators of organic matter in soil, which is a vital component of any terrestrial ecosystem (Batjes 1996). Soil nitrogen is often a limiting factor in plant growth, which is offset by surface application of fertiliser on farmland. However, applying fertiliser is expensive, particularly for poor farmers in less economically developed countries (Nkonya, Schroeder & Norman 1997), and can cause environmental problems associated with nitrate leeching (Di & Cameron 2005; Macdonald et al. 1989). If farmers can rely on ecosystem services to sequester and release soil nitrogen and carbon, fertiliser application can be reduced (Power 2010; Swinton et al. 2007).

The potential for some fossorial invertebrates, such as earthworms, to provide ecosystem services is well-studied (Blouin et al. 2013; Lavelle et al. 2006). However, no study has yet focused on burrowing spiders, such as Idiopidae, and their contribution to soil nitrogen and carbon content. New Zealand Idiopidae are known to drop food remains and shed skins into middens at the bottoms of their burrows (Irish 2001) which, upon decomposition, may gradually leech nitrates and organic carbon into the surrounding deep soil. For a preliminary study, soil nitrogen and carbon content levels were measured from soil samples taken within a population of *Cantuaria curtisi*, and compared with soil nitrogen and carbon levels adjacent to the population.

30 cm soil cores were taken from four *Cantuaria curtisi* burrows and four adjacent areas, approximately two, three, four, and five metres from the last burrow found in the population. to test whether *Cantuaria* burrows may have a detectable impact on soil nitrogen and carbon levels. Percentage soil carbon and nitrogen was measured using an air-dried and ground subsample of each soil core using an Elementar Vario-Max CN Elemental Analyser (Elementar GmbH, Hanau, Germany).

Results (Figs. A1.2 and A1.3) showed a gradient in soil nitrogen and carbon from the northernmost burrow sample to the southernmost burrow sample along Hoon Hay Valley Road (S 43°35'38.1" E 172°36'15.0"). Carbon percentage varied from 6.36% to 2.95% within the

Cantuaria population (mean = 4.28%). Carbon percentage varied from 2.6% to 1.99% in the control samples. Nitrogen percentage varied from 0.52 to 0.26% within the *Cantuaria* population (mean = 0.36). Nitrogen percentage varied from 0.25 to 0.20% in the control samples.

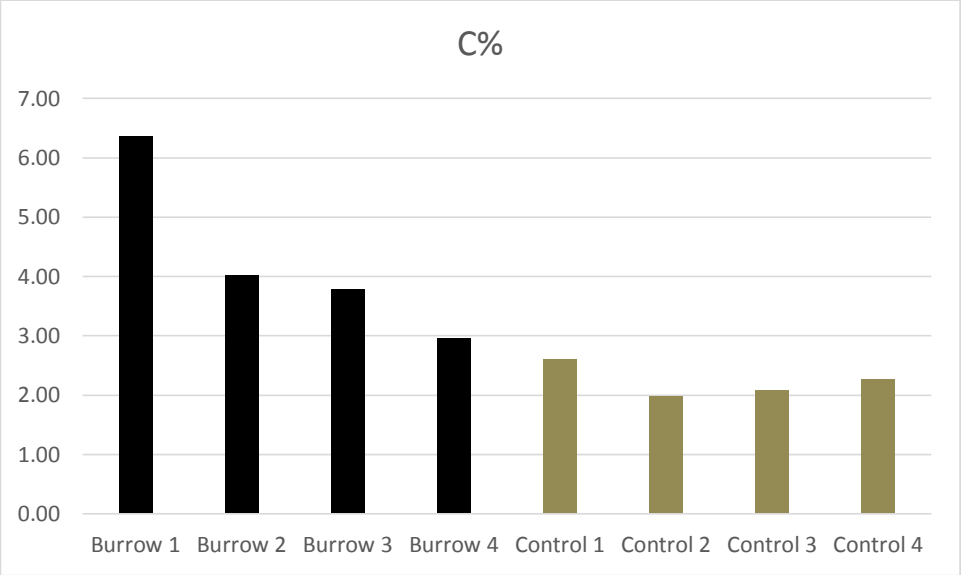

Figure A1.2: Carbon levels found within and adjacent to a population of *Cantuaria curtisi*. Black bars marked Burrow 1-Burrow 4 show samples taken from within the *Cantuaria* population, while grey bars marked Control 1- Control 4 show samples taken from adjacent to the population. The first bar (Burrow 1) is the northernmost sample, and the samples were taken progressively further south until Control 4, which is the southernmost sample.

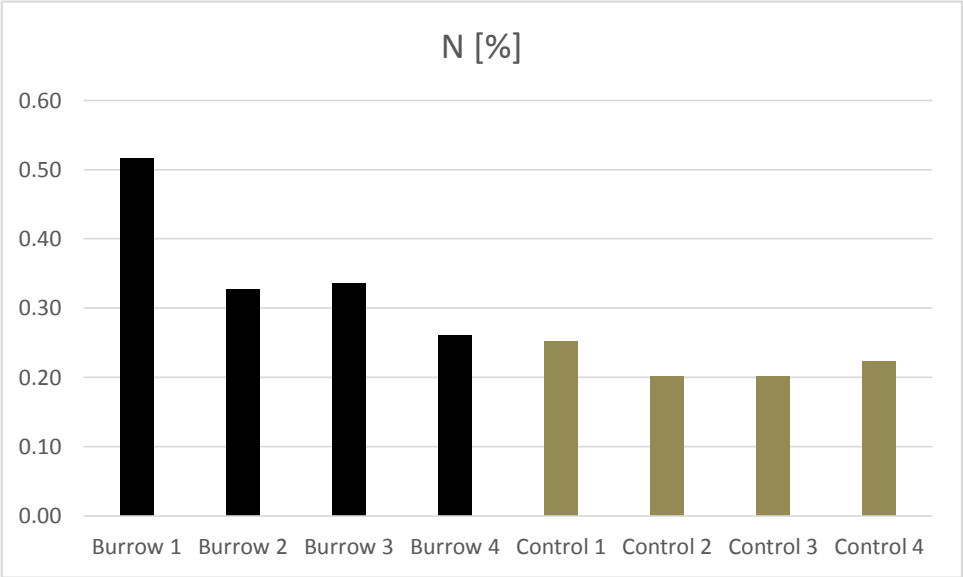

Figure A1.3: Nitrogen levels found within and adjacent to a population of *Cantuaria curtisi*. Black bars marked Burrow 1-Burrow 4 show samples taken from within the *Cantuaria* population, while grey bars marked Control 1- Control 4 show samples taken from adjacent to the population. The first bar (Burrow 1) is the northernmost sample, and the samples were taken progressively further south until Control 4, which is the southernmost sample.

Nitrogen and carbon levels were higher within the population of *Cantuaria* than the levels adjacent to the population. However, there is a gradient between the highest levels of carbon and nitrogen in the northernmost burrow and the lowest levels in the southernmost burrow. Interestingly, this gradient does not appear to be present outside the population. The small sample size, and its spatial autocorrelation, make determination of the cause of variation in nitrogen and carbon levels difficult. Perhaps the first burrow was closer to the middle of the population, where most carbon and nitrogen had entered the soil from burrow deposits. However, the first burrow may also have been closest to a different source of carbon and nitrogen, such as a rotted animal or plant. The soil type may have changed imperceptibly from north to south, for example to a sandier soil which may hold less carbon or nitrogen (Tiessen, Stewart & Bettany 1982). The pattern seen in this dataset may also be caused by natural variation in carbon and nitrogen levels; this natural variation may appear as a pattern due to the small sample size in this preliminary study. However, the nitrogen and carbon data do indicate that nitrogen and carbon levels are elevated within this *Cantuaria* population, which may be caused by prey remains and faecal matter deposited at the bottom of the burrow.

Future research into the effect of *Cantuaria* presence on the soil could build on my preliminary study by taking more samples from more populations. Samples should be taken at random from areas within, and adjacent to, all sides of the population. Samples could also be taken progressively further away from the population to find out how great an area is covered by the increase (if such an increase exists) in soil carbon and/or nitrogen. If a correlation exists between soil's proximity to burrows and its carbon and/or nitrogen content, causation may be detected or rejected in a controlled captive study. The captive study would involve *Cantuaria* kept in an ecological microcosm and fed beetles weekly. A beetle-only control microcosm would have beetles added to it at the same rate and in the same number as they are fed to spiders. Having beetles but no spiders simulates a wild scenario in which invertebrates are present but trapdoor spiders are absent. A soil-only control microcosm would have soil but no invertebrates added. Soil samples could then be taken from the three microcosms from the soil surface and deeper (3.g. 30 cm deep) into the soil. Samples would be taken before, during, and after the study to see how the nitrogen and carbon levels fluctuate depending on treatment. The three microcosms could be compared using a generalised linear mixed model to see if spider presence had an impact on soil carbon and nitrogen levels in different depths of soil. Decomposing matter produced by the insects may elevate carbon and nitrogen levels closer to the soil surface, while *Cantuaria* burrows may elevate the nutrient levels deeper in the soil due to their burrows.

A.3 Adaptive cluster sampling

Adaptive cluster sampling was conducted following the protocol by Thompson (1990) to determine the size and spread of *Cantuaria* populations around Canterbury. Quadrats of two m^2 were used. However, adaptive cluster sampling was found to be an unsuitable method of

determining population spread and size in *Cantuaria* due to the cryptic nature of the burrows (meaning that absences could not always be confirmed) and the variety of terrain inhabited (including deep bush and grassland, which was difficult to search for burrows).

A.4 Captive management of *Cantuaria* species

Initial attempts at keeping adult New Zealand Idiopidae from Invercargill, Christchurch, and Takaka used soil from near the individuals' burrows or clay soil from another location. The soil substrate was packed into 23 cm high mason jars and moistened with tap water. The spiders were placed into the jars, but they remained on the surface of the soil; later, holes were made with a pen. Spiders occasionally went into the holes, but would not move or eat. Any trapdoor lids that were made were poorly constructed of loose soil and silk. The spiders died after approximately one month in captivity. One juvenile individual from Nelson survived for approximately four months in a bucket of clay soil. The bucket was maintained indoors. The juvenile made a lidded burrow and took mealworms as feed. After a month of feeding the juvenile, it no longer fed and the lid was not replaced when it was removed. Some specimens from Invercargill were kept in a cardboard tube filled with cotton wool, as spider burrows were observed in the cotton wool in which they had been transported. However, the spiders remained on the surface of the cotton wool in the cardboard tube, without feeding or building burrows; they died after approximately two weeks.

A later attempt at keeping captive *Cantuaria* spp. for venom milking was based on informal trapdoor spider care guidelines for an African idiopid colloquially known as the red trapdoor spider (PhillyAquaponics 2014; Tansley 2013). Mason jars 22 cm in depth were filled with peat, gently packed down, up to 2cm below the brim. The peat was thoroughly soaked in tap water until the water level was above the soil level, then allowed to dry for a week until the surface of the soil was moist to the touch but not wet. A hole roughly 10 cm deep was made in the soil with a pen. Wider holes were made to accommodate larger spiders. The soil was packed tightly around the hole to avoid collapse. The spider was deposited near the hole so that it could go directly inside. Squares of cloth fastened with elastic bands were used to cover the mouths of the jars. At the beginning of the captive management trial, squares of food wrap (pierced with air holes) were fastened over the jar mouths; one particularly large (30 mm long) and aggressive female specimen escaped overnight, having made a large hole in the food wrap covering.

Packed peat appeared to be a better substrate than clay soil or cotton wool, as the spiders lived between eight months and two years in the peat. Three spiders were maintained in a 15°C controlled temperature room with normal day–night light cycles. Six spiders were maintained under a car port in Christchurch. Water was poured onto the substrate once a month to moisten the soil, and the spiders were fed weekly with *Tenebrio molitor* beetles, apart from one three-month period over the summer, during which they were not fed or watered. Two of the

Invercargill spiders built lids on their previously lidless burrows during the summer. If a lid was destroyed, the spiders would build another. Some spiders widened their burrows and built chambers against the glass sides of the jar, through which the spider could be observed during the day. Some individuals dug at the peat to create a light, aerated soil surface.

A.5 Venom milking

Live spiders were obtained and maintained in captivity for venom extraction to observe the properties of *Cantuaria* venom. Time and resources did not allow for any analysis of venom properties aside from a Bradford assay (Bradford 1976) to check for protein presence and concentration. However, venom collection techniques are provided here for the benefit of future research.

Initial attempts were made to antagonise spiders with plastic sticks, so that the spider would bite the stick which could then be inserted into a tube containing a 10% phosphate buffered saline (PBS) solution. However, spiders frequently overshot the plastic stick, and the large amount of PBS solution required to house the plastic stick caused the venom to become highly diluted.

A second trial involved Parafilm M (Bernis Company, Wisconsin, USA) stretched over the mouths of 1.5 ml plastic vials, in which 0.1 ml of ice-cold PBS was placed (filtered through a syringe filter). The spider was antagonised until it lunged, at which point the mouth of the vial was thrust towards it and its fangs were guided into the centre of the Parafilm. The fangs normally became stuck in the Parafilm, and the spider was further antagonised until venom was no longer seen to be coming from its fangs. The spider was then removed carefully by hand and replaced in its container. Most Christchurch and Takaka spiders would readily attack the Parafilm, but occasionally an individual had to be lifted by hand and its fangs guided into the Parafilm, at which point venom could be seen to ooze from the fangs. Venom in the PBS solution was frozen immediately and maintained at -20°C. Milking of spiders through Parafilm may shield the venom sample from soil, vomit, and other contaminants, as the Parafilm forms a barrier against the spider's mouth. Any soil on the fangs is likely to be brushed off as the fangs insert into the Parafilm. Invercargill and Dunedin spiders could not be milked for venom, as they would not attack the vials and would remain still or attempt to escape. If lifted by hand, the Invercargill and Dunedin spiders would not expose their fangs sufficiently for insertion into the Parafilm. However, electrostimulation of the venom glands would likely be successful in extracting venom from the Dunedin and Invercargill spiders.

Venom extraction by milking spiders through Parafilm (similar to the way snakes are milked for snake antivenom production; World Health Organization 2010) may be an effective method of obtaining venom from large spiders. However, other methods of spider milking using electrostimulation may be required to obtain larger quantities of venom, particularly from smaller spider species; however, measures must be taken when using any method of venom

extraction to avoid contamination (G.J. Binford 2001; Greta J Binford & Wells 2003; Rocha-e-Silva, Sutti & Hyslop 2009).

Appendix B

List of papers included in biogeographic metaanalysis (Chapter 3) and their attributes

Results	Author conclusion	Taxon age	Presumed taxon age	Lead author surname	Author region	Publication year	Taxon type	Dispersal ability	Habitat type	Food type	Ecosystem zones	Body weight adult	Body weight dispersal
dispersal	dispersal	1	1	Biffin	other	2010	gymnosperm	medium	specialist	none	1	200000	0.0001
dispersal	dispersal	1	1	Teeling	other	2005	mammal	medium	generalist	generalist	6	0.015	0.015
dispersal	dispersal	1	1	Krosch	other	2011	insect	high	generalist	generalist	2	0.0001	0.0001
dispersal	dispersal	1	1	Jordan	other	2010	angiosperm	medium	generalist	none	4	0.5	0.0001
dispersal	dispersal	1	1	Perrie	NZ	2007	pteridophyte	high	generalist	none	7	0.5	0.0001
dispersal	dispersal	1	1	Perrie	NZ	2005	pteridophyte	high	generalist	none	5	0.5	0.0001
dispersal	dispersal	1	1	Nielsen	other	2010	lizard	low	generalist	generalist	8	0.1	0.1
dispersal	dispersal	1	1	Heinrichs	other	2005	bryophyte	high	generalist	none	5	0.1	0.0001
dispersal	dispersal	1	1	Knapp	NZ	2005	angiosperm	medium	generalist	none	4	50000	0.0001
dispersal	dispersal	1	1	Johansson	other	2011	bird	medium	generalist	generalist	5	0.3	0.3
dispersal	dispersal	1	1	Goldberg	NZ	2011	bird	high	generalist	generalist	7	0.7	0.7
dispersal	dispersal	1	1	Chacon	other	2012	angiosperm	medium	generalist	none	4	0.3	0.0001
dispersal	dispersal	1	1	Thomas	other	2014	angiosperm	medium	generalist	none	4	0.3	0.0001
dispersal	dispersal	1	1	Waters	NZ	2007	mollusc	high	generalist	generalist	11	0.001	0.0001
dispersal	dispersal	1	1	Chapple	NZ	2009	lizard	medium	generalist	generalist	12	0.2	0.2
dispersal	dispersal	1	1	Pons	other	2011	insect	medium	generalist	generalist	5	0.0001	0.0001
dispersal	dispersal	1	1	Pratt	NZ	2008	insect	medium	generalist	generalist	18	0.001	0.0001
dispersal	dispersal	1	1	Trewick	NZ	2005	insect	medium	generalist	generalist	18	0.001	0.0001
Zealandian	Zealandian	2	2	Krosch	other	2013	insect	high	generalist	generalist	5	0.0001	0.0001
Zealandian	Zealandian	2	2	Lessard	other	2013	insect	high	generalist	generalist	7	0.0001	0.0001
dispersal	dispersal	1	1	Thornhill	other	2015	angiosperm	high	generalist	none	14	0.0001	0.0001
Zealandian	Zealandian	2	2	Colloff	other	2014	Arachnid	low	generalist	generalist	3	0.0001	0.0001

Zealandian	vicariance	2	3	Rheindt	other	2014	bird	high	generalist	generalist	4	0.8	0.8
Zealandian	Zealandian	2	2	Allegrucci	other	2010	insect	low	generalist	generalist	9	0.001	0.0001
vicariance	vicariance	3	3	Liebherr	other	2011	insect	low	generalist	generalist	2	0.0001	0.0001
vicariance	vicariance	3	3	Edgecombe	other	2008	other.arthropod	low	generalist	generalist	5	0.0001	0.0001
vicariance	vicariance	3	3	Cranston	other	2010	insect	high	generalist	generalist	4	0.0001	0.0001
vicariance	vicariance	3	3	Wilson	other	2008	crustacean	low	specialist	generalist	1	0.4	0.0001
vicariance	vicariance	3	3	Boyer	other	2009	Arachnid	low	generalist	generalist	4	0.0001	0.0001
vicariance	vicariance	3	3	McDowall	NZ	2005	crustacean	medium	generalist	generalist	3	0.3	0.0001
vicariance	vicariance	3	3	Allwood	NZ	2010	Onychophoran	low	generalist	generalist	6	0.0001	0.0001
Zealandian	vicariance	2	3	Wright	other	2008	bird	high	generalist	generalist	6	150	150
Zealandian	vicariance	2	3	Lee	NZ	2012	angiosperm	high	generalist	generalist	2	0.1	0.0001
vicariance	vicariance	3	3	Mitchell	NZ	2012	angiosperm	high	generalist	none	4	0.1	0.0001
dispersal	dispersal	1	1	Renner	other	2010	angiosperm	high	generalist	none	4	0.1	0.0001
vicariance	vicariance	3	3	Sun	other	2014	bryophyte	high	generalist	none	3	0.01	0.0001
vicariance	vicariance	3	3	Beu	NZ	2014	mollusc	high	generalist	generalist	2	0.01	0.0001
vicariance	vicariance	3	3	Buckley	NZ	2010	insect	low	generalist	generalist	6	0.0001	0.0001
vicariance	vicariance	3	3	Toon	other	2010	crustacean	medium	generalist	generalist	3	0.4	0.0001
vicariance	vicariance	3	3	Jones	other	2008	tuatara	medium	generalist	generalist	4	0.8	0.8

B.1 List of papers

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Appendix C

List of historically collected specimens examined and referred to in Chapter 6.

Otago Museum

Catalogue No	Species designation	Type	Collection locality	Collection Date	Collector	Notes
IV10871	*Cantuaria; Cantuaria vellosa; vellosa*	Allotype/Type Specimen	Kakanui/Waitaki District/Otago/New Zealand	1966		
IV10872	*Cantuaria; Cantuaria borealis; borealis*	Holotype/Type Specimen	Price's Bush/Canterbury/New Zealand		R.R. Forster	
IV23181	*Cantuaria*		Galloway/Central Otago District/Otago/New Zealand	03 Oct 1997	Mr Anthony Harris	Hexathelid, not *Cantuaria*
IV23182	*Cantuaria dendyi*		Banks Peninsula/Banks Peninsula District/Canterbury/New Zealand	20 Sep 1973		
IV23183	*Cantuaria*		Ashburton/Ashburton District/Canterbury/New Zealand	09 Dec 1974	S Brown	
IV23184	*Cantuaria*		Stewart Island/Southland/New Zealand	01 Aug 1971	Alan Wright	

IV23185	*Cantuaria magna*	Moana/Westland District/West Coast/New Zealand	01 Dec 1973	A McFarlane
IV23186	*Cantuaria*	Earnscleugh Station/Central Otago District/Otago/New Zealand	06 Jan 1975	L Robertson
IV23187	*Cantuaria*	Wellington/New Zealand	03 Aug 1966	Dick Wilton
IV23188	*Cantuaria*	Catlins/Clutha District/Otago/New Zealand	31 Aug 1966	Forster & Wilton
IV23189	*Cantuaria*	New Zealand	01 Mar 1973	
IV23190	*Cantuaria huttoni*	Akatore Creek/Clutha District/Otago/New Zealand	14 Apr 1966	Dick Wilton
IV23191	*Cantuaria*	Lawrence/Clutha District/Otago/New Zealand	10 Oct 1966	Dick Wilton
IV23196	*Cantuaria*	Dunback/Waitaki District/Otago/New Zealand	24 Sep 1967	Dick Wilton
IV23197	*Cantuaria*	Kyeburn/Central Otago District/Otago/New Zealand	16 Dec 1967	Dick Wilton
IV23198	*Cantuaria*	New Zealand	21 Jun 1971	Don Laing
IV23201	*Cantuaria*	Hakataramea Valley/Hakataramea/Waimate	29 Sep 1970	G. Mason

		District/Canterbury/New Zealand		
IV23203	*Cantuaria*	Tasman District/Tasman/New Zealand	21 Jun 1971	S While
IV23204	*Cantuaria*	Rangiora/Waimakariri District/Canterbury/New Zealand	01 Mar 1980	I Stephenson
IV23205	*Cantuaria*	Oban/Stewart Island/Southland/New Zealand	01 May 1979	J Carico
IV23206	*Cantuaria*	Taieri Ridge/Dunedin City/Otago/New Zealand	06 Dec 1967	Dick Wilton
IV23207	*Cantuaria huttoni*	Leith Saddle/Dunedin City/Otago/New Zealand	28 Aug 1973	Sue Forster
IV23208	*Cantuaria*	Orepuki/Southland District/Southland/New Zealand	20 Nov 1970	Forster & Wilton
IV23210	*Cantuaria*	Kaituna Valley/Banks Peninsula/Banks Peninsula District/Canterbury/New Zealand	13 Apr 1967	Forster & Wilton
IV23211	*Cantuaria*	Enfield/Waitaki District/Otago/New Zealand	20 May 1967	Prof. Brian Marples
IV23212	*Cantuaria*	Enfield/Waitaki District/Otago/New Zealand	20 May 1967	Prof. Brian Marples

IV23213	*Cantuaria huttoni*	Trotters Gorge/Waitaki District/Otago/New Zealand	26 Jul 1967		
IV23214	*Cantuaria*	Ettrick/Central Otago District/Otago/New Zealand	16 Mar 1972	A Turner	
IV23215	*Cantuaria*	Central Otago/Otago/New Zealand	14 Oct 1967	Dick Wilton	
IV23217	*Cantuaria*	Logan Burn/Central Otago District/Otago/New Zealand	15 Dec 1982	Barratt	
IV23218	*Cantuaria*	Logan Burn/Central Otago District/Otago/New Zealand	03 Nov 1982	Barratt	
IV23219	*Cantuaria*	Logan Burn/Central Otago District/Otago/New Zealand	03 Nov 1982	Barratt	
IV23220	*Cantuaria*	Logan Burn/Central Otago District/Otago/New Zealand	02 Dec 1982	Barratt	Adult males
IV23221	*Cantuaria*	Logan Burn/Central Otago District/Otago/New Zealand	15 Dec 1982	Barratt	Adult male and female

IV23222	*Cantuaria huttoni*		03 Dec 1965		Female
IV23223	*Cantuaria*	Dunedin/Dunedin City/Otago/New Zealand	18 Feb 1980	Mr Anthony Harris	Not *Cantuaria.* juvenile *Hexathele*?
IV23224	*Cantuaria*	Wanganui/Wanganui District/Wanganui-Manawatu/New Zealand	20 May 1984	David Hay	1 adult female, 1 female possibly juvenile.
IV23225	*Cantuaria reeftonensis*	Westland District/West Coast/New Zealand	01 Jan 1951	J Veale	Female
IV23226	*Cantuaria cambridgei*	Oamaru/New Zealand	May 1950	B. J. Marples	Male
IV23227	*Cantuaria regalicus*	Windsor/Waitaki District/Otago/New Zealand	01 Aug 1965	Prof. Brian Marples	Female
IV23228	*Arbanitis dendyi*	Port Hills/Canterbury/New Zealand	Mar-71	Forster	Female.
IV23229	*Arbanitis dendyi*	Akaroa/Banks Peninsula/Canterbury/ New Zealand	1954	C. sinclair	Females
IV23319	*Arbanitis insulanus*	D'Urville Island	21-Aug-60	M. Williams	Adult female and 3 juveniles.
IV23230	*Arbanitis dendyi*	Springfield/Canterbury/ New Zealand	1954	M. Warren	Adult males
IV23231	*Arbanitis dendyi*	Governors Bay/Banks Peninsula/Canterbury/ New Zealand	21-Jan-49	R. Cresswell	Female. Specimen covered in debris so difficult to see all features, but only 4 sigillae could be found, and spinnerets unusually pointed and held vertically - possibly not *Cantuaria*.

IV23232	*Cantuaria dendyi*		Akaroa/Banks Peninsula/Canterbury/ New Zealand	1954		Females
IV23233	*Arbanitis reductus*		Oxford/Canterbury/New Zealand	10-May-62	J. M. Kelsey	Female.
IV23235	*Arbanitis sinclairi*		Moana/Westland District/West Coast/New Zealand	Jan-54	C. sinclair	Female.
IV23236	*Arbanitis sinclairi*		Moana/Westland District/West Coast/New Zealand	10-Apr-50	M. Warren	Female.
IV23237	*Arbanitis apertus*		Waipiata/Central Otago District/Otago/New Zealand	21-Mar-55	Mrs. Weir	Adult male
IV23238	*Arbanitis magnus*		Greymouth/Grey District/West Coast/New Zealand	22-Dec-36	Forster	Females
IV23239	*Arbanitis johnsi*		South Terrace/Karamea/Nelson /New Zealand	Jan-54	R. R. Forster	Male
IV23240	*Arbanitis johnsi*		Takaka Hill/Nelson/New Zealand	03-Feb-63	A. Walker	Female
IV23241	*Arbanitis johnsi*	Allotype/Type Specimen	Rockville/Nelson/New Zealand	10-Oct-39	H. Withington	Female
IV23242	*Arbanitis gilliesii*		Duntroon/Waitaki District/Canterbury/New Zealand	05-May-47	B. J. Marples	Female
IV23243	*Arbanitis gilliesii*		Kia ora Cnr/Enfield/Otago/New Zealand		B. J. Marples	Female

IV23244	*Arbanitis gilliesii*	Ridge Road/Oamaru/New Zealand	06-Nov-65	B. J. Marples	Female
IV23245	*Cantuaria gilliesii*	Kia ora Cnr/Enfield/Otago/New Zealand	1966	B. Marples	Female
IV23246	*Arbanitis depressus*	East of Clydevale/Central Otago/New Zealand	09-May-65	B. J. Marples	Female
IV23247	*Arbanitis vellosus*	Kakanui/Waitaki District/Otago/New Zealand		B. J. Marples	Female
IV23248	*Cantuaria huttoni*				Juvenile
IV23249	*Cantuaria huttoni*				
IV23250	*Cantuaria huttoni*				Juvenile
IV23251	*Cantuaria huttoni*	Dunedin/Dunedin City/Otago/New Zealand			Adult male
IV23252					Juvenile
IV23253					Juvenile
IV23254		Taieri Mouth/Southland/New Zealand			Female
IV23255		Trotters Gorge/Waitaki District/Otago/New Zealand			1 juvenile 4 female
IV23256	*Cantuaria huttoni*	Dunedin/Dunedin City/Otago/New Zealand	16 May 1981	Court	Adult female

IV23258	*Arbanitis myersi*	Johnsonville/Wellington/ New Zealand	06-Dec-41	R. R. Forster	Adult female
IV23259	*Arbanitis myersi*	Levin/Wellington/New Zealand	06-May-48	R. R. Forster	Adult female
IV23260	*Arbanitis myersi*	Botanical gardens/Wellington/ New Zealand	20-Mar-41	F. A. Bodley	Adult female
IV23261	*Arbanitis myersi*	Karori Hills/Wellingtin[sic]/New Zealand	12-Feb-61	R. R. Forster	1 adult female, 1 juvenile.
IV23262	*Arbanitis magnus*	Greymouth/Grey District/West Coast/New Zealand		A.W. Parrott	Adult male
IV23263	*Arbanitis magnus*	Greymouth/Grey District/West Coast/New Zealand	04-Apr-56	L. R. Jackson	Males
IV23264	*Arbanitis catlinensis*	Papatowai/Clutha District/Otago/New Zealand	11-Jan-61	R. R. Forster	3 adult females plus 1 miscellaneous araneomorph
IV23265	*Arbanitis orepukiensis*	Orepuki/Southland District/Southland/New Zealand	09-May-49	R. R. Forster	1 adult female, 1 juvenile.
IV23266	*Arbanitis orepukiensis*	Longwood Range/Southland District/Southland/New Zealand	25-Nov-48	J. H. Sorensen	2 adult females, 1 juvenile.
IV23267	*Arbanitis orepukiensis*	Tuatapere/Southland/ New Zealand	19-May-62	B. J. Marples	Adult female plus miscellaneous araneomorph

IV23268	*Arbanitis sylvaticus*	Thompson Sound/Fiordland/ Southland/New Zealand	14-Jan-48	R. R. Forster	Adult female
IV23270	*Cantuaria toddi*	Cromwell/Central Otago District/Otago/New Zealand	25 Feb 1977		
IV23282	*Arbanitis dendyi*	Kennedys Bush/Christchurch/New Zealand	15-Apr-49	Pat Cahill	Adult male
IV23284	*Arbanitis dendyi*	Christchurch/ Christchurch City/Canterbury/New Zealand	06-May-49	W.H. Dukes	Adult male
IV23286	*Arbanitis dendyi*	Taylors Mistake/Canterbury/ New Zealand	01-Aug-50	G. A. Knox	Adult male
IV23289	*Arbanitis dendyi*	Governors Bay/Banks Peninsula/Canterbury/ New Zealand	14-Apr-49	R. Cresswell	Adult female and adult male
IV23291	*Cantuaria stewarti*	Stewart Island/Southland/New Zealand	01 Jan 1952	Allan	Female with 2 juveniles.
IV23292	*Cantuaria stewarti*	Golden Bay/Stewart Island/Southland/New Zealand	01 Jan 1959	Dr Morris Watt	
IV23293	*Cantuaria stewarti*	Halfmoon Bay/Stewart Island/Southland/New Zealand	30 May 1955		

IV23294	*Cantuaria stewarti*	Stewart Island/Southland/New Zealand	1898	Mr Walter Traill	
IV23295	*Cantuaria stewarti*	Halfmoon Bay/Stewart Island/Southland/New Zealand	01 Jun 1950	Allan	
IV23296	*Cantuaria stewarti*	Halfmoon Bay/Stewart Island/Southland/New Zealand	01 Apr 1949	Allan	
IV23297	*Cantuaria stewarti*	Halfmoon Bay/Stewart Island/Southland/New Zealand	10 Mar 1948	Allan	
IV23298	*Cantuaria stewarti*	Halfmoon Bay/Stewart Island/Southland/New Zealand	14 Mar 1949	Allan	
IV23299	*Cantuaria stewarti*	Halfmoon Bay/Stewart Island/Southland/New Zealand	14 Mar 1949	Allan	
IV23300	*Cantuaria stewarti*	Golden Bay/Stewart Island/Southland/New Zealand	15 Nov 1961	R.R. Forster	juvenile
IV23301	*Cantuaria stewarti*	Golden Bay/Stewart Island/Southland/New Zealand	01 Jan 1961	Dr Morris Watt	2 juveniles 1 adult female
IV23302	*Cantuaria stewarti*	Stewart Island/Southland/New Zealand	23 Nov 1946	R.R. Forster	
IV23303	*Cantuaria stewarti*	Stewart Island/Southland/New Zealand	22 Apr 1957	Prof. Brian Marples	

IV23304	*Cantuaria stewarti*	Stewart Island/Southland/New Zealand	20 Nov 1947	Allan	female
IV23305	*Cantuaria stewarti*	Stewart Island/Southland/New Zealand	1920	Mr Walter Traill	Adult male
IV23306	*Cantuaria*	Lawrence/Clutha District/Otago/New Zealand			
IV23307	*Cantuaria*	Dunedin/Dunedin City/Otago/New Zealand	15 Jan 1971	Mr Anthony Harris	
IV23308	*Cantuaria*	Logan Burn/Central Otago District/Otago/New Zealand		Barratt	
IV23309	*Cantuaria*	Halfmoon Bay/Stewart Island/Southland/New Zealand	01 Jan 1948	Allan	
IV23310	*Cantuaria*	Stewart Island/Southland/New Zealand	28 Jan 1955	Dell	
IV23311	*Cantuaria*	Stewart Island/Southland/New Zealand	31 Oct 1960	R.G. Ordish	
IV23312	*Cantuaria huttoni*	Stewart Island/Southland/New Zealand			
IV23313	*Cantuaria*	Southland District/Southland/New Zealand			

IV23314	*Cantuaria*		Tasman District/Tasman/New Zealand	20 Oct 1977	J McBurney	adult males
IV23315	*Cantuaria*		Westport/Westland District/West Coast/New Zealand	20 Feb 1949		
IV23316	*Cantuaria*		Westland District/West Coast/New Zealand	12 Jan 1944	A.W. Parrott	
IV23317	*Cantuaria*		West Coast/New Zealand		J Moore	Definitely *Cantuaria,* impossible to determine species without DNA. Probably *C. johnsi* or *C. magna*.
IV23322	*Cantuaria huttoni*		Leith Saddle/Dunedin City/Otago/New Zealand	28 Aug 1973	Sue Forster	Juvenile male araneomorph, not *Cantuaria.* Also accompanied by an amphipod.
IV23333	*Cantuaria*		Ilam/Christchurch City/Canterbury/New Zealand	15 Apr 1994	John Huub	Large, dark adult male, unusual palps - probably new species.
IV3309	*Cantuaria apica*	Holotype/Type Specimen	Maungatua/Dunedin City/Otago/New Zealand	28 Feb 1947	Prof. Brian Marples	
IV3310	*Cantuaria orepukiensis*	Holotype/Type Specimen	Orepuki/Southland District/Southland/New Zealand	21 May 1962	Prof. Brian Marples	
IV3311	*Cantuaria orepukiensis*	Allotype/Type Specimen	Longwood Range/Southland	17 May 1948	J.H. Sorensen	

			District/Southland/New Zealand			
IV3312	*Cantuaria minor*	Holotype/Type Specimen	Oban/Stewart Island/Southland/New Zealand	Mar 1960	G. Collett	
IV3313	*Cantuaria sylvatica*	Holotype/Type Specimen	Thompson Sound/Fiordland/ Southland/New Zealand	14 Jan 1958	R.R. Forster	
IV3314	*Cantuaria isolata*	Holotype/Type Specimen	Whero Island/Foveaux Strait/Southland/New Zealand		Prof. Brian Marples	
IV3315	*Cantuaria catlinsensis*	Holotype/Type Specimen	Papatowai/Clutha District/Otago/New Zealand	11 Jan 1961	R.R. Forster	
IV3316	*Cantuaria; Arbanitis collensis; collensis*	Holotype/Type Specimen	Bench Island/Foveaux Strait/Southland/New Zealand		Miss Valerie Todd	
IV3317	*Cantuaria allani*	Holotype/Type Specimen	Halfmoon Bay/Stewart Island/Southland/New Zealand	14 Mar 1949	Allan	Female
IV3318	*Cantuaria; Arbanitis huttoni; huttoni*	Neotype/Type Specimen	Dunedin/Dunedin City/Otago/New Zealand		Miss Valerie Todd	
IV3319	*Cantuaria; Arbanitis huttoni; huttonii*	Neotype/Type Specimen	Dunedin/Dunedin City/Otago/New Zealand		Miss Valerie Todd	

IV3320	*Cantuaria maxima*	Holotype/Type Specimen	Hakataramea/Waimate District/Canterbury/New Zealand	29 Aug 1948	Prof. Brian Marples
IV3321	*Cantuaria magna*	Holotype/Type Specimen	Greymouth/Grey District/West Coast/New Zealand	06 Feb 1955	A.C. Quy
IV3322	*Cantuaria magna*	Allotype/Type Specimen	Greymouth/Grey District/West Coast/New Zealand	10 Aug 1948	A.R. Thompson
IV3323	*Cantuaria prina*	Holotype/Type Specimen	Westport/Westland District/West Coast/New Zealand	Apr 1949	R.M. Elley
IV3324	*Cantuaria toddi*	Holotype/Type Specimen	Cromwell/Central Otago District/Otago/New Zealand	07 Nov 1958	R.R. Forster
IV3325	*Cantuaria toddi*	Allotype/Type Specimen	Alexandra/Central Otago District/Otago/New Zealand	14 Feb 1965	Prof. Brian Marples
IV3326	*Cantuaria kakanuiensis*	Holotype/Type Specimen	Kakanui/Waitaki District/Otago/New Zealand	Mar 1965	Prof. Brian Marples
IV3327	*Cantuaria; Arbanitis assimilis; gilliesii*	Allotype/Type Specimen	Palmerston/Waitaki District/Otago/New Zealand		Miss Valerie Todd
IV3328	*Cantuaria depressa*	Holotype/Type Specimen	South Otago/Otago/New Zealand	09 May 1965	Prof. Brian Marples
IV3329	*Cantuaria vellosa*	Holotype/Type Specimen	Kakanui/Waitaki District/Otago/New Zealand	01 Apr 1957	Prof. Brian Marples

IV3330	*Cantuaria aperta*	Holotype/Type Specimen	Waipiata/Central Otago District/Otago/New Zealand	21 Mar 1955	Mrs Weir
IV3331	*Cantuaria pilama*	Holotype/Type Specimen	Balclutha/Clutha District/Otago/New Zealand	1914	W.D. Blair
IV3332	*Cantuaria; Maoriana dendyi; dendyi*	Holotype/Type Specimen	Christchurch/Christchurch City/Canterbury/New Zealand		Miss Valerie Todd
IV3333	*Cantuaria; Maoriana dendyi; dendyi*	Allotype/Type Specimen	Christchurch/Christchurch City/Canterbury/New Zealand		Miss Valerie Todd
IV3334	*Cantuaria sinclairi*	Holotype/Type Specimen	Moana/Westland District/West Coast/New Zealand	10 Apr 1950	M. Warren
IV3335	*Cantuaria cognata*	Holotype/Type Specimen	Waimate/Waimate District/Canterbury/New Zealand	10 Sep 1952	T. McKenzie
IV3336	*Cantuaria myersi*	Holotype/Type Specimen	King George V Memorial Park/Wellington/Wellington City/Wellington/New Zealand	05 Feb 1955	A. Richards
IV3337	*Cantuaria myersi*	Allotype/Type Specimen	King George V Memorial Park/Wellington/Wellington City/Wellington/New Zealand	05 Feb 1955	A. Richards
IV3338	*Cantuaria medialis*	Holotype/Type Specimen	Mount Taraka/Marlborough District/Marlborough/New Zealand		C. Talbot

IV6147	*Cantuaria dunedinensis*	Holotype/Type Specimen	Princes Street/Dunedin/Dunedin City/Otago/New Zealand	08 May 1959	Harwood
IV6148	*Cantuaria assimilis*	Holotype/Type Specimen	Palmerston/Waitaki District/Otago/New Zealand		Prof. Brian Marples
IV6149	*Cantuaria wanganuiensis*	Holotype/Type Specimen	Makirikiri/Wanganui District/Wanganui-Manawatu/New Zealand		V Todd
IV6151	*Cantuaria; Arbanitis marplesi; marplesi*	Holotype/Type Specimen	Duntroon/Waitaki District/Canterbury/New Zealand		

Other museum specimens (catalogue numbers unknown)

Museum	Date collected	Species diagnosis	Collector	Collecting location	Gender
Lincoln University	June 1993	*Cantuaria sp. - very long spinnerets so not sure on the ID*	A. C. Leckie	Lincoln University	male – very long spinnerets so not sure on the ID
Lincoln University	Dec 1989-Jan1990	*Cantuaria sp.*	J. W. Early	Prices Valley, Banks Pen. (collected in yellow pan trap)	female
Lincoln University	June 2001	*Misgolas sp.*	A. G. Stokes	Broad Oaks, Chch in water on patio	male
Lincoln University	Dec 1989-Jan1990	*Cantuaria sp.*	J. W. Early	Prices Valley, Banks Pen. (collected in yellow pan trap)	female

Lincoln University	Jan 1993	*Cantuaria sp.*	C. J. Vink	Christchurch (dug up in garden)	female
Lincoln University	Dec 1989–Jan1990	*Cantuaria sp.*	J. W. Early	Prices Valley, Banks Pen. (collected in yellow pan trap)	female
Lincoln University	July 1996	*Misgolas parrotti*	C. J. Vink & A. B. Freeman	Lincoln University, drowned in artificial pond	male
Lincoln University	April–May 1998	*Misgolas reducta (?)*	A. E. Singleton (ID by C. J. Vink)	Lords Bush, Springfield (pitfall trap)	male
Lincoln University	April–May 1998	*Misgolas reducta (?)*	A. E. Singleton (ID by C. J. Vink)	Lords Bush, Springfield (pitfall trap)	male
Lincoln University	April–May 1998	*Misgolas reducta (?)*	A. E. Singleton (ID by C. J. Vink)	Lords Bush, Springfield (pitfall trap)	male
Lincoln University	Dec 1989–Jan1990	*Cantuaria sp.*	J. W. Early	Prices Valley, Banks Pen. (collected in yellow pan trap)	female
Lincoln University	Sept 1996	*Misgolas parrotti*	M. H. Bowie & C. J. Vink	Lincoln University farm pitfall traps under Macrocarpa hedge	subadult female
Lincoln University	Jan 1983	*Cantuaria sp.*	B. I. P. Barratt	Logan Burn 900m	male
Lincoln University	March 2000	*Misgolas napua*	A. C. Harris	Willowbridge, south Canterbury, lidded burrow	
Lincoln University	July 2000	*Misgolas dendyi*	Sue Worner (ID by A. McLaehlan)	Lincoln in inside water bowl	male
Lincoln University	March 2000	*Misgolas vellosa*	A. C. Harris	Waiana karua, in lidded burrow	female
Natural History Museum London	1903	*Misgolas dendyi*	Hogg	Christchurch	female
Natural History	1924	*Cantuaria dendyi*		Taylor's Mistake	male

Museum London				
Natural History Museum London	1928	*Misgolas huttoni*	Otago	female
Natural History Museum London	n.d.	*Cantuaria dendyi*	Quail Island	female and juveniles
Natural History Museum London	1903	*Misgolas gilliesi*	Christchurch	female
Natural History Museum London	1924	*Misgolas huttoni*	Stewart Island	female

Appendix D

List of specimens regarded as new species by this thesis

Species	Type status	Gender	Collection location	Collector name
C. viridaria	Holotype	female	Williams Park, Days Bay, Wellington	V.R. Smith
C. viridaria	Paratype	female	Williams Park, Days Bay, Wellington	V.R. Smith
C. viridaria	Paratype	female	Williams Park, Days Bay, Wellington	V.R. Smith
C. viridaria	Paratype	female	Williams Park, Days Bay, Wellington	V.R. Smith
C. viridaria	Paratype	female	Williams Park, Days Bay, Wellington	V.R. Smith
C. attenborough i	Paratype	female	Conroys Road, Central Otago	V.R. Smith
C. attenborough i	Paratype	female	Conroys Road, Central Otago	V.R. Smith
C. attenborough i	Holotype	female	Conroys Road, Central Otago	V.R. Smith
C. attenborough i	Paratype	female	Conroys Road, Central Otago	V.R. Smith
C. attenborough i	Paratype	female	Conroys Road, Central Otago	V.R. Smith
Cantuaria insidia	Holotype	female	Greymouth	V.R. Smith
C. mcquillani	Allotype	female	Denniston	V.R. Smith
C. mcquillani	Holotype	male	Denniston	B. McQuillan
C. pollocki	Holotype	female	Duntroon	V.R. Smith
C. pollocki	Paratype	female	Duntroon	V.R. Smith
C. olartei	Holotype	female	Jacksons Road, Marlborough	V.R. Smith, J. Cooper, J. Stitchbury
C. olartei		female	Jacksons Road, Marlborough	V.R. Smith, J. Cooper, J. Stitchbury
C. vinki	Holotype	female	Kingwell Drive, Blenheim	S. Lyon
C. irishae	Holotype	female	Le Bons Bay, outside school	V.R. Smith
C. lawryi		male	Dyers Pass Road, Cashmere	P. Cochrane
C. lawryi	Holotype	female	Worsleys Road, Christchurch	M. Provis, C.J. Vink, V.R. Smith
C. curtisi	Holotype	female	Hoon Hay Valley Road	V.R. Smith
C. curtisi	Paratype	female	Hoon Hay Valley Road	V.R. Smith
C. curtisi	Paratype	female	Hoon Hay Valley Road	V.R. Smith
C. curtisi	Paratype	female	Hoon Hay Valley Road	V.R. Smith

C. hithaeglirensis	Holotype	female	Kennedys Bush	V.R. Smith
C. hithaeglirensis	Paratype	female	Kennedys Bush	V.R. Smith
C. hithaeglirensis	Paratype	female	Kennedys Bush	V.R. Smith
C. fountainae	Holotype	male	Eyrewell	M. Bowie
C. fountainae		male	West Melton	P. Johns
C. fountainae	Allotype	female	Lincoln	S. Moore
C. fountainae		female	Eyrewell	M. Bowie
C. fountainae		female	Eyrewell	M. Bowie
C. fountainae		male	West Melton	P. Johns
C. fountainae		male	Lincoln	D. Leeh
C. fountainae		male	Lincoln	C. B. Phillips
C. fountainae		male	Eyrewell	M. Bowie
C. fountainae		male	Eyrewell	M. Bowie

Appendix E

Spinneret morphology of new species described in Chapter 6

***Cantuaria* species**	**Length ratio of lateral pair:medial pair of spinnerets**
C. attenboroughi	35:6
C. curtisi	16:3
C. fountainae	37:12
C. insidia	62:17
C. viridaria	16:3
C. hithaeglirensis	47:8
C. vinki	Unknown
C. McQuillani	Male: 35:11 Female: 25:7
C. pollocki	Unknown
C. olartei	7:2
C. irishae	Unknown
C. lawryi	5:1

Appendix F

Fa: Populations represented in phylogenies in Chapter 5

Specific epithet	Specimen IDs	Collection date	Location	COI accession numbers	ITS accession numbers	CytB accession numbers	Number of H3 sequences	Specimens deposited	Holotype deposited
fountainae	BN1-BN6	04/07/2014	Eyrewell	KY615639-K615643	MF425904-MF425908	MF425883 MF425884	3	CANTY	CANTY
fountainae	BN7-BN9	04/07/2014	S43°38'31.0" E172°28'06.5"	KY615638, KY615644	MF425903		3	CANTY	CANTY
fountainae	CD1	01/04/2014	S43°38'36.8" E172°28'04.0" (+/-200 m)	KY615630			0	CANTY	CANTY
Unknown	CD2	01/04/2014	Christchurch	KY615659			0	LENZ	
lawryi	CD2female	26/04/2014	S43°34'43.0" E172°37'50.0"				1	CANTY	CANTY
sylvatica	CQ1-4	29/04/2014	S45°27'51.9" E167°09'56.3"		MF425900		1	LENZ	
borealis	DB1	13/11/2012	Bankside, Canterbury				1	LENZ	
magna	HM1	29/01/2011	S40°49'43.2" E173°00'22.2"	KY615618	MF425928		1	LENZ	
fountainae	JN1-5	03/03/2014	S43°31'52.2" E172°22'07.8"	KY615614, KY615614			0	CANTY	CANTY
vinki	LD1	11/11/2014	S41°30'21.6" E173°56'21.0"	KY615662			0	CANTY	CANTY
Unknown	LF1	17/07/2015	S43°30'55.6" E172°31'23.8"		MF425933		1	LENZ	
fountainae	MD1-MD3	28/03/2014	S43°38'39.0" E172°28'15.0" (+/-55m)	KY615627-KY615629	MF425919, MF425920		3	CANTY	CANTY

mcquillani	MJ1	21/02/2014	S41°44'06.0" E171°46'54.0"	KY615651			0	CANTY	CANTY
prina	MJ2	13/11/2014	S41°01'26.4" E172°55'22.8"				1	LENZ	
kakahuensis	My1	06/11/2014	S44°09'10.2" E171°05'36.3"	KY615634			0	LENZ	
Unknown	My2, My3	06/11/2014	S44°05'22.5" E171°14'15.1"		MF425910		1	LENZ	
fountainae	ND1	05/05/2015	S43°38'31.0" E172°28'06.5"				1	CANTY	CANTY
dendyi	PD2	14/12/2013	S43°34.813', E172°36.657'	KY615658			1	LENZ	
lawryi	PD3	14/12/2013	S46°57'33.2" E168°07'32.2"	KY615657	MF425894	MF425885	1	CANTY	CANTY
dendyi	PD5, PD6	14/12/2013	S43°34.837', E172°36.811'				1	LENZ	
fountainae	PN1	22/06/2012	S43°38'22.2" E172°28'28.8"	KY615626			0	CANTY	CANTY
kakanuiensis	SA1, SA2	01/04/2014	Kakanui	KY615632, KY615633	MF425914, MF425915		2	LENZ	
apica	Sb1, Sb2	03/04/2014	S45°52'52.4" E170°09'18.5"				1	LENZ	
curtisi	SD1, SD5–8	19/03/2014	S43°35'38.1" E172°36'15.0"	KY615656	MF425895–MF425898		3	CANTY	CANTY
delli	Sd1	02/06/2014	S46°46.11', E167°39.01'				1	LENZ	
delli	Sd1–5	02/06/2014	S46°46.15', E167°39.15'		MF425899		0	LENZ	
hithaeglirensis	SD2–SD4	20/03/2014	S43°37'33.4" E172°37'23.9"	KY615631	MF425916–MF425918		1	CANTY	CANTY
irishae	SD9	15/04/2014	S43°45'37.5" E173°03'13.3"	KY615663	MF425891		0	MONZ	MONZ
Unknown	SE2	30/03/2014	S44°35'54.0" E170°38'09.1"		MF425913	MF425886	1	LENZ	
napua	SF1–3	26/03/2014	S45°01'43.8" E170°51'32.2"	KY615645			0	LENZ	

assimilis	Sh1, Sh2, Sh3, Sh5	02/04/2014	S45°28'49.3" E170°43'13.3"	KY615619			0	LENZ	
Unknown	SH1, SH2	05/04/2014	Taieri Mouth near S46°01'04.7" E170°10'30.7"		MF425925-MF425927		0	LENZ	
insulana	SI1	13/05/2014	S40°53'26.1" E173°51'41.4"	KY615646	MF425902		1	LENZ	
Unknown	SJ12	07/05/2014	S41°15'45.4" E173°17'54.1"				1	LENZ	
olartei	SJ13	09/02/2014	S41°30'08.3" E173°52'37.0"	KY615660, KY615661	MF425893	MF425887	1	CANTY	CANTY
mcquillani	SJ14, SJ16	07/06/2014	S41°43'07.3" E171°46'28.9"	KY615650	MF425901		2	CANTY	CANTY
insidia	SJ15	08/09/2014	S42°28'31.9" E171°11'10.8"	KY615637	MF425912		1	CANTY	CANTY
Unknown	SN11	16/09/2014	Waitaki				1	LENZ	
attenboroughii	SN2-SN6	19/04/2014	S45°16'28.6" E169°20'06.4"	KY615620-KY615622	MF425924	MF425879, MF425880	5	CANTY, BM	CANTY
Unknown	SN7-9, SN10, SN13	12/09/2014	S44°50'07.5" E170°28'45.2"		MF425909		4	LENZ	
Unknown	SO1-5	18/04/2014	S46°07'37.6" E167°40'22.4"		MF425929		4	LENZ	
Unknown	SP1-4	04/06/2014	Golden Bay, South Island				1	LENZ	
prina	SP5, SP6	08/06/2014	S41°45'21.1" E171°36'05.9"	KY615611, KY615612	MF425931		1	LENZ	
Unknown	Sr1	06/04/2014	S46°11'34.8" E169°45'37.4"	MF425890			1	LENZ	
pollocki	SR2	31/03/2014	S 44°56'15.9" E170°36'55.1"	KY615648			1	OTM	LENZ
pilama	Sr3	06/04/2014	S46°13'09.0" E169°43'50.5"	KY615664			0	LENZ	
pollocki	SR4	30/03/2014	S 44°56'15.9" E170°36'55.1"	KY615647			0	OTM	LENZ
toddi	ST1	21/04/2014	S45°17'55.6" E169°27'04.1"	KY615668			0	LENZ	

Unknown	St1	16/04/2014	S46°33'07.6" E169°28'50.1"				1	LENZ	
Unknown	St2-St4	16/04/2014	S46°33'07.6" E169°28'50.1"				3	LENZ	
Unknown	SU2	14/04/2014	S46°54'12.6" E168°07'16.6"		MF425911		0	LENZ	
vellosa	SV2, SV3	28/03/2014	Awamoko	KY615666, KY615667			0	LENZ	
wanganuiensis	SW1, SW2, SW8	23/05/2014	S39°52'48.1" E175°15'02.8"	KY615615-KY615617			0	LENZ	
viridaria	SW3-6	19/05/2014	S41°16'48.1" E174°54'26.4"	KY615652			0	OTM	MONZ
depressa	SX1, SX4, SX5, SX7	28/12/2013	S46°7'57.58" E169°31'24.47"	KY615653-KY615655, KY615665	MF425889		0	LENZ	
myersi	SY1, SY2	19/05/2014	S41°13'41.6" E174°47'28.8"	KY615635, KY615636		MF425888	1	LENZ	
johnsi	VJ1	29/01/2011	S40°49'57.1" E173°00'31.6"	KY615623	MF425923		1	LENZ	
Unknown	WU3, WU4, WU6, WU5, WU7, WU8	09/04/2014	S46°57'33.2" E168°07'32.2"		MF425892	MF425881	1	LENZ	
Unknown	WU9	08/04/2014	S46°53'58.5" E168°07'48.3"			MF425882	1	LENZ	
isolata	WZ1	11/04/2014	S46°54'46.6" E168°12'21.2"		MF425932		0	LENZ	
Misgolas (outgroup)	OG1		Australia	KY615624			0		
Misgolas (outgroup)	OG2		Australia	KY615625	MF425921		0		
Misgolas (outgroup)	OG3		Australia		MF425922		0		

Note: H3 sequences uploaded onto FigShare (https://figshare.com/articles/H3cantuariaalignment_fas/5208403) due to some sequences having low quality chromatogram data at base pair positions 241, 246, 247 and 248.

Fb: Other *Cantuaria* specimens referred to in this thesis

Specific epithet	Specimen ID	Collection date	Location	Specimens deposited
borealis	BB1	02/03/2011	Port Hills	LENZ
dendyi	BD5	02/03/2011	S43°35'23.9" E172°39'47.0"	LENZ
dendyi	BD6	02/03/2011	S43°35'23.9" E172°39'47.0"	LENZ
dendyi	BD7	02/03/2011	S43°35'23.9" E172°39'47.0"	LENZ
dendyi	BD8	02/03/2011	S43 35.398 E172 39.784	LENZ
Unknown	CN1	02/10/2014	S46°25'40.5" E168°21'57.4"	LENZ
Unknown	CN2	02/10/2014	S46°25'40.5" E168°21'57.4"	LENZ
Unknown	CN3	02/10/2014	S46°25'40.5" E168°21'57.4"	LENZ
Unknown	EN1	Unknown	Invercargill	LENZ
gilliesi	JG1	15/02/2015	S46.29043°, E169.92785°	LENZ
Unknown	JN6	29/07/2015	S46°25'31.3" E168°25'58.6"	LENZ
Unknown	MJ3	13/11/2014	S40°50'53.1" E172°52'15.2"	LENZ
Unknown	MJ4	13/11/2014	S40°50'53.1" E172°52'15.2"	LENZ
Unknown	MJ5	13/11/2014	S40°50'53.1" E172°52'15.2"	LENZ
Unknown	QI1	17/09/2015	S43°37'45.2" E172°41'48.9"	LENZ
Unknown	QI2	17/09/2015	S43°37'45.2" E172°41'48.9"	LENZ
Unknown	QI3	17/09/2015	S43°37'45.2" E172°41'48.9"	LENZ
Unknown	QI4	17/09/2015	S43°37'45.2" E172°41'48.9"	LENZ
Unknown	Sa1	28/03/2014	S44°43'33.7" E171°02'15.5"	LENZ
Unknown	Sa2	28/03/2014	S44°43'33.7" E171°02'15.5"	LENZ
Unknown	Sa3	28/03/2014	S44°43'33.7" E171°02'15.5"	LENZ
apica	Sb2	03/04/2014	S45°52'52.4" E170°09'18.5"	LENZ
curtisi	SD10	27/12/2014	S43°35'38.1" 172°36'15.0"	LENZ
curtisi	SD11	27/12/2014	S43°35'38.1" E172°36'15.0"	LENZ
curtisi	SD12	27/12/2014	S43°35'38.1" E172°36'15.0"	LENZ
Unknown	SD13	11/06/2015	S43°48'45.5" E172°57'26.8"	LENZ

Unknown	SD14	11/06/2015	S43°48'45.5" E172°57'26.8"	LENZ
Unknown	SD15	11/06/2015	S43°48'45.5" E172°57'26.8"	LENZ
Unknown	Se1	24/09/2014	S43°17'06.1" E172°09'56.6"	LENZ
Unknown	SE1	31/03/2014	S44°48'32.4" E170°31'36.0"	LENZ
Unknown	SE3	30/03/2014	S44°35'54.0" E170°38'091"	LENZ
Unknown	SE4	30/03/2014	S44°35'54.0" E170°38'081"	LENZ
Unknown	SE5	31/03/2014	Gards Road, Otekaike	LENZ
Unknown	SE6	31/03/2014	Gards Road, Otekaike	LENZ
Unknown	SG1	27/04/2014	Oamaru	LENZ
Unknown	SG2	27/04/2014	Oamaru	LENZ
Unknown	SG3	27/04/2014	Oamaru	LENZ
Unknown	SH5	05/04/2014	S46°01'04.7" E170°10'30.7"	LENZ
Unknown	SJ1	03/06/2014	S41°17'45.1" E173°15'58.5"	LENZ
Unknown	SJ10	08/05/2014	S41°16'20.3" E173°15'36.3"	LENZ
Unknown	SJ11	08/05/2014	S41°16'20.3" E173°15'36.3"	LENZ
Unknown	SJ2	03/06/2014	S41°17'45.1" E173°15'58.5"	LENZ
Unknown	SJ3	07/05/2014	S41°15'45.4" E173°17'54.1"	LENZ
Unknown	SJ4	08/05/2014	S41°16'20.3" E173°15'36.3"	LENZ
Unknown	SJ5	07/05/2014	S41°16'20.3" E173°15'36.3"	LENZ
Unknown	SJ6	05/05/2014	S41°03'08.5" E172°57'46.1"	LENZ
Unknown	SJ7	05/05/2014	S41°03'08.5" E172°57'46.1"	LENZ
Unknown	SJ8	05/05/2014	S41°03'08.5" E172°57'46.1"	LENZ
Unknown	SJ9	08/05/2014	S41°16'20.3" E173°15'36.3"	LENZ
Unknown	SK1	08/05/2014	Nelson	LENZ
Unknown	SN1	10/05/2014	S41°53'56.8" E171°26'21.9"	LENZ
Unknown	SN12	18/09/2014	S44°36'53.3" E171°08'40.7"	LENZ
Unknown	SR1	30/03/2014	S44°56'15.9" E170°36'55.1"	LENZ
Unknown	SS1	06/05/2014	S40°44'05.8" E172°38'08.3"	LENZ
Unknown	SS2	06/05/2014	S40°44'05.8" E172°38'08.3"	LENZ
Unknown	SS3	06/05/2014	S40°44'05.8" E172°38'08.3"	LENZ
Unknown	ST2	21/04/2014	S45°17'55.6" E169°27'04.1"	LENZ

wanganuiensis	SW7	23/05/2014	S39°52'48.1" E175°15'02.8"	LENZ
depressa	SX6	28/12/2013	S46°7'57.58" E169°31'24.47"	LENZ
myersi	SY3	19/05/2014	S41°13'41.6" E174°47'28.8"	LENZ
myersi	SY4	19/05/2014	S41°13'41.6" E174°47'28.8"	LENZ
Unknown	SY6	19/05/2014	S41°14'42.3" E174°47'06.6"	LENZ
Unknown	SY7	19/05/2014	S41°14'42.3" E174°47'06.6"	LENZ
myersi	SY8	19/05/2014	S41°13'41.6" E174°47'28.8"	LENZ
collensis	WC1	13/04/2014	S46°54'24.9" E168°13'58.5"	LENZ
collensis	WC2	13/04/2014	S46°54'24.9" E168°13'58.5"	LENZ
collensis	WC3	13/04/2014	S46°54'24.9" E168°13'58.5"	LENZ
collensis	WC4	13/04/2014	S46°54'24.9" E168°13'58.5"	LENZ
Unknown	WH1	05/03/2013	S45°48'27" E170°31'27"	LENZ
Unknown	WH10	11/11/2014	S45°51'32" E170°80'26"	LENZ
Unknown	WH2	15/04/2014	S45°48'41" E170°25'22"	LENZ
Unknown	WH3	21/04/2014	S46°04'06" E169°49'38"	LENZ
Unknown	WH4	29/05/2014	S45°16'20" E170°43'54"	LENZ
Unknown	WH5	27/05/2014	S46°16'54" E169°53'02"	LENZ
Unknown	WH6	28/01/2013	S46°23'02" E169°46'23"	LENZ
Unknown	WH7	16/04/2014	S45°42'32" E170°32'51"	LENZ
Unknown	WH8	16/04/2014	S45°42'32" E170°32'51"	LENZ
Unknown	WH9	04/04/2014	S45°51'32" E170°80'26"	LENZ
Unknown	WO1	23/11/2013	S46°21'20" E168°01'34"	LENZ
Unknown	WO2	10/12/2013	S46°06'36" E167°41'06"	LENZ
Unknown	WO3	23/11/2013	S46°21'21" E168°00'31"	LENZ
Unknown	WO4	10/12/2013	S46°01'50" E167°42'54"	LENZ
Unknown	Wt1	24/01/2013	S46°29'27" E169°30'10"	LENZ
Unknown	Wt2	22/02/2013	S46°33'03.36" E169°28'47.11"	LENZ
Unknown	Wt3	24/01/2013	S46°29'27" E169°30'10"	LENZ
Unknown	Wt4	27/01/2013	S46°28'30" E169°28'47"	LENZ

Unknown	Wt5	28/01/2013	Tautuku	LENZ
Unknown	Wt6	22/02/2013	S46°35'10" E169°23'08"	LENZ
Unknown	WU1	08/04/2014	S46°53'58.5" E168°07'48.3"	LENZ
Unknown	WU2	14/04/2014	S46°53'43.6" E168°09'39.1"	LENZ
isolata	WZ2	11/04/2014	S46°54'46.6" E168°12'21.2"	LENZ

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